THE SCIENCE OF PAIR-BONDING AND FUTURE DIRECTIONS

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THE SCIENCE OF PAIR-BONDING AND FUTURE DIRECTIONS

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EDITORIAL
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Editorial: The Science of Pair-Bonding and Future Directions

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Keywords: pair bonding, close relationships, romantic relationships, dating, marriage, attachment, evolutionary psychology

Editorial on the Research Topic

The Science of Pair-Bonding and Future Directions

The goal of this Research Topic (RT) was to bring together broad scholarship on the science of pair-bonding and to inform future directions for research on this topic. Many who study pair- bonds do so within particular disciplines and/or sub-disciplines, often focusing efforts and contributing to knowledge on specific species, behaviors, conceptualizations, mechanisms, theories, levels of analyses, and more recently large data sets available via the rise of online dating. This Research Topic serves as a launch-pad for broader discussions that enable us to learn from one another, cross-pollinate, strengthen our ideas, and nurture interdisciplinary work that advances research on pair-bonding.

Two articles in this RT present original research that highlights the modern landscape of human pair-bonding. Levy et al. use massive mobile dating data from over 421 million potential matches to investigate dating preferences. Their study showed that similarity of characteristics–such as psychological traits, physical traits, personal choices (i.e., desiring the same relationship type), and shared experiences–predicted dating matches. Mogilski et al. utilize life history theory (LHT) as a framework to understand the moral stigma associated with consensual non-monogamy (CNM). The authors found that individuals in CNM relationships are more likely to report a fast-life history which is linked to being viewed negatively based on inaccurate beliefs about risk and negative outcomes.

Four articles in this RT examine human pair-bonding with studies that include neuroimaging methodology. Tsapelas et al. examined the attractiveness of relationship alternatives by manipulating self-expansion in two studies (one behavioral, one fMRI) with participants in committed relationships. The studies showed that priming the "need for self-expansion" led to better memory for attractive alternatives with traits dissimilar to their partner, and that priming with partner self-expansion led to less fMRI BOLD responsiveness to attractive alternatives (compared with a love prime and a neutral prime). Azhari et al., examine how personality traits and closeness influence brain responses in the prefrontal cortex (PFC) when viewing social interactions. The authors utilize fNIRS methodology and find differences in PFC based on openness, closeness, and the perceived type of social interaction (romantic partners, siblings, friends). Acevedo et al. explore the neural and genetic correlates of romantic love in newlyweds across the first year of marriage genetic analysis (*AVPR1a* rs3, *OXTR* rs53576, *COMT* rs4680, and *DRD4*-7R), and self-reported relationship quality. Their findings establish the importance of the reward system in romantic love and highlight the biological substrates that facilitate the maintenance of romantic love in early-stage marriages.

Two articles in this RT focus on pair bonding in non-human animals. Potretzke and Ryabinin provide a mini-review of the prairie vole (*Microtus ochrogaster*: a socially monogamous rodent), the

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neurobiology of pair-bonding, and the effects of addictive substances on pair-bonding in the prairie vole as well as in humans. Savidge and Bales present data from two experiments with titi monkeys (*Plecturocebus cupreus*) investigating responses to separation from attachment figures and adult affiliative behavior. Their research showed that decreased infant locomotor behavior in the presence, as opposed to the absence, of a primary attachment figure was related to decreased anxiety-like behavior in adult pair-mates during a novelty response task. The authors conclude that titi monkeys are an appropriate animal model for attachment research.

Finally, three papers in this RT are reviews or theoretical pieces on human pair-bonding. Prior reviews the literature on behavioral synchrony and highlights how using synchrony as a framework leads to a better understanding of pair-bonding across timescales, contexts, and species. Branand et al. review the literature on the inclusion of the other in the self (IOS), including measurement, predictors, and outcomes of IOS, within the context of long-term monogamous pair-bonds in humans, and other important relationship factors (e.g., positive affect, perspective-taking, self-disclosure, shared excitement). They also review recent theoretical work extending traditional understandings of IOS and propose future directions for IOS research and the self-expansion model. Goetz et al. examine evolutionary mismatch in human mating studies. They suggest that human research participants are often non-representative and WEIRD (Western, Educated, Industrialized, Rich, and Democratic). Goetz et al. identify and review the literature on nine additional mismatch characteristics and highlight the STRANGELY WEIRD-ness of participants (interact with Social media, engage in Temporary relationships, can Relocate with relative ease, have Autonomy in mate choice, are Nulliparous, experience social Group segmentation, are being tested in an Educational setting, have Lots of options, and are Young adults). Their article showcases the importance of considering evolutionary mismatch in mating research and provides recommendations for future studies.

Collectively, the articles in this RT on the science of pair-bonding highlight the complexity of this field. It includes work on the synchrony of behavior among couples, synchronization, and similarity in dating choices, and more complicated issues such as the social stigma attached to consensual non-monogamy. It also explores complex psychological factors in romantic relationships such as "inclusion of others in the self" and the need for self-expansion among individuals for making pair-bonding choices and its influence on the desire for alternative partners. Both human and non-human animal studies in this RT provide scientific advances in understanding the biology of pair-bonding, highlighting the importance of reward as well as more complicated processes, such as intimacy and cognition. These studies highlight both basic and complex processes–such as genetic underpinnings, higher-order cognition, and behaviors–which mediate the proclivity to sustain pair-bonds. In sum, the works in this RT highlight the prevailing importance of pair-bonds in humans and other species as they influence biology, behavior, emotions, psychological processes, and complicated processes such as the perception of merging with another and the motivation to expand the self. This RT also highlights the need to widen the scope of practical knowledge to include diverse samples of individuals in relationship studies. Collectively, these works show us that relationship science has made marked strides in advancing our understanding of the complexities of the basic nature of pair-bonds, and they also provide important considerations for future research.

AUTHOR CONTRIBUTIONS

Both authors have contributed to the writing of this editorial.

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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ORIGINAL RESEARCH
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Polar Similars: Using Massive Mobile Dating Data to Predict Synchronization and Similarity in Dating Preferences

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Leveraging a massive dataset of over 421 million potential matches between single users on a leading mobile dating application, we were able to identify numerous characteristics of effective matching. Effective matching is defined as the exchange of contact information with the likely intent to meet in person. The characteristics of effective match include alignment of psychological traits (i.e., extroversion), physical traits (i.e., height), personal choices (i.e., desiring the same relationship type), and shared experiences. For nearly all characteristics, the more similar the individuals were, the higher the likelihood was of them finding each other desirable and opting to meet in person. The only exception was introversion, where introverts rarely had an effective match with other introverts. When investigating the preliminary stages of the choice process we looked at the consistency between the choice of men/women, the time it took users to make these binary choices, and the tendency of yes/no decisions. We used a biologically inspired choice model to estimate the decision process and could predict the selection and response time with nearly 60% accuracy. Given that people make their initial selection in no more than 11 s, and ultimately prefer a partner who shares numerous attributes with them, we suggest that users are less selective in their early preferences and gradually, during their conversation, converge onto clusters that share a high degree of similarity in characteristics.

Keywords: online dating applications, decision making, homophily, big data, matching

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INTRODUCTION

Online dating has become one of the most popular methods for single individuals to meet and develop relationships (Madden and Lenhart, 2006; Valkenburg and Peter, 2007; Finkel et al., 2012). As early as 2005, over a third of single Internet users were using online dating services. Within the 2 years that followed, more new romantic relationships had begun as a byproduct of online services than through any other means, with the exception of meeting through friends (Finkel et al., 2012). The usage of mobile applications (apps) for dating has nearly tripled, and apps are predicted to continue growing in the following years (Juniper Research, 2015). Currently, dating apps exist for users as young as those in their teens and as senior as those in their eighties and nineties.

Traditional online dating sites (OkCupid, Match.com, JDate, etc.) focus on allowing users to create extensive profiles with photos and a multitude of fields for self-description. Typically, once a user creates their profile, they can search through the profiles of potential romantic partners in the hope of communicating and eventually meeting in person. Contemporary mobile dating apps (Tinder, Hinge, Bumble, etc.) use recommendation algorithms to present users with a stack of potential matches that are believed to have the highest likelihood of connecting in a meaningful way. On these apps, each potential romantic interest is displayed one at a time with a photo and basic information, such as age and location. A user can click on the profile being presented and see additional information. This may include height, religious beliefs, hometown, various interests, and a short bio. Users have the option to either reject or accept the person as a potential match but cannot view the next potential match until they have made a selection. Once two users confirm their interest in one another they are both notified and are able to communicate. By 2016, over 60% of the mobile app dating market included this type of selection process (Statista.com, 2016).

Many mobile apps are populated with information by pulling data from the user's social media account (typically, Facebook), rather than having users manually fill out extensive profiles. This provides a wealth of knowledge previously unavailable for traditional online dating services. Additionally, this provides a higher confidence in the user's identity, age, hometown, current city, occupation, education, etc. (Duguay, 2017). In the case of Hinge, which we will focus on throughout this paper, users are *required* to log in using Facebook, but can choose to manually enter additional information that is not available on Facebook, such as the type of relationship they are open to (i.e., "Casual") or the religion they identify with. While many mobile dating apps do not require users to enter additional information about their height, political preferences, personality, etc., popular apps such as Tinder and Bumble have fields titled "about me" or "bio" that users commonly use to add these attributes. None of the popular mobile dating apps, including Hinge, require these data. However, Hinge does have dedicated fields for these attributes which make queries about them easy to evaluate.

Given that these apps make the preliminary selection of a partner a binary decision, they provide an environment that lends itself to quantitative decision making models. This is contrary to traditional online dating sites where the choice of a partner is harder to analyze and model due to the breadth and depth of information users are exposed to in the context of their decision making.

In this work, we investigate the selection process and look at the level of similarity between two individuals, across various attributes, as a driver of the ultimate match—that is, how attributes that pertain to a person (their height, religious affiliation, education, preferences, socio-economic status, or personality traits) indicate the likelihood that they will prefer to interact with others who share similar attributes. We show that people who are similar to one another tend to prefer each other and are more likely to actually engage in a conversation that leads to meeting in person.

We break the matching process into two stages and analyze each one separately in different sections of the paper. In the first half of the paper, we look at the choice to exchange contact information with another user after both people have expressed initial interest in one another, and some communication has happened through the app's chat platform. This choice relates to the decision to potentially interact with the other person outside of the dating app.

In the second half of the paper, we investigate the binary choice to pursue an initial interaction with a potential candidate by merely signaling an interest in communication. In the world of mobile app dating this is typically noted as "swiping right" [on a picture of the candidate]. This choice happens first, typically followed by a conversation using the app chat platform, and then ending with a decision to interact outside the app sandbox.

Whereas the decision to swipe right is a binary yes/no decision reflecting a general interest in the other person, the exchange of information could be based on more knowledge about that person (including knowledge of expressed interest and potentially some additional information that was disclosed during the communication). Additionally, the choice to exchange contact information typically involves more commitment (i.e., disclosing personal revealing details). The choice to exchange contact information that leads to a meeting can also be seen as a choice between a broader set of options. The person is not just choosing whether they are interested in learning more about another individual online, they are choosing whether they want to spend time with them, at the expense of spending time with others, for what is typically a longer period. Therefore, this choice is seen as more involved.

Prior works looking at partner choices in the context of similarity and homophily—the tendency of individuals to associate and bond with similar others—have shown that such homophily permeates in marriage, friendship, and various interpersonal relationships (McPherson et al., 2001). Generally, the preference toward similar others was shown in the context of the similarity/attraction theory. The theory suggests that individuals tend to be attracted to those who are similar to themselves. This was demonstrated in the context of shared attitudes (e.g., views regarding family), personality traits (i.e., extroversion, neuroticism, etc.) (Youyou et al., 2017), physical attractiveness (Bruch and Newman, 2018), socio-economic status, religious beliefs, habits, ethnicity, and intelligence (Byrne, 1971; McPherson et al., 2001). Focusing on marriage, Schwartz (2013) suggested that partners tend to ultimately resemble one another on various features such as age, education, race, and more (Bruch and Newman, 2018). Contrarily, some research has focused on the notion that "opposites attract." Observation by Winch and Goodman (1968) on compatibility among married couples suggested that some complementary, yet opposite, characteristics may lead to more successful long-term relationships. Recent research suggests that differences in personality can increase novelty and personal growth in the early stages of a relationship, leading to a more fulfilling dating experience (Finkel, 2017).

Additional works in the context of partner choice have explored the notion of an ideal standards model (ISM). ISM suggests that people consider a partner for a close relationship based on three factors: warmth-trustworthiness, vitality-attractiveness, and status-resources (Fletcher et al., 1999; Fletcher and Simpson, 2000), regardless of whether they possess those themselves. ISM predicts that people would end up more satisfied in relationships where their partner is perceived as aligned with their own ideal standard (Fletcher et al., 1999; Campbell et al., 2001; Buyukcan-Tetik et al., 2017) rather than if the partner is similar to them.

Some biological studies of mate selection seem to support the fact that the compatibility between partners is not likely to be at the level of exhibited attributes such as socio-demographic or socio-economic features, but rather at a genetic level. For example, Andersson and Simmons (2006) discuss immune system diversity as a driver of pairing. Another example suggests that opposite genetic profiles may drive attraction more than their manifested phenotypes (Santos et al., 2005). According to these studies, people with opposing characteristics may find each other attractive and desirable despite mounting personality differences because of attributes that are not directly visible to them.

While all these dimensions of a person could play a part in the pairing choice, due to the fact that dating is shifting from in person meeting to online discovery, the initial selection is now often based on basic information that is acquired remotely, in a short time window of seconds. This simplification reduces the number of dimensions a person can consider in partner selection and provides an opportunity to quantify the effects of specific attributes on the likelihood that couples will match.

In this work, we focus our investigation on features of a user's mobile dating app profile and ask which are most effective in drawing a match between two people. Using the limited information provided to users when making a selection (name, a picture, location, school, relationship intentions, common friends) we try to estimate the likelihood of a pair choosing to exchange contact information and engage in a conversation outside the digital world. While we recognize that many encounters in the real world would still end up as a non-effective match, our scope is solely confined to the measure of initial success as defined by the app users—to translate the online correspondence into correspondence outside the virtual world (Gibbs et al., 2006).

Our work contributes to the growing body of literature identifying key characteristics in mating that lead to more desired relationships, offers tools to optimize the algorithms enabling the dating app world, and potentially aids in navigating the journey toward a successful match. Additionally, our results shed light on the app-based dating horizon which seems to reflect the preferred method of meeting potential partners for the younger generation (ages 16–38). This is the age group that yields the highest revenues in digital domains in the Western world (Smith, 2015) and, accordingly, is sought after by many corporations.

MATERIALS AND METHODS

Data

Data were gathered from Hinge (Hinge Inc.; New York, NY, United States), a popular dating application used across the two most popular mobile platforms (iPhone and Android). Among all dating platforms (including non-mobile ones), Hinge is ranked 14, with 1.1% of total dating platform users. This included records for more than half a million users and hundreds of millions of entries prior to November 2015. Overall, the data reflect interactions among users in 38 cities in the United States, England, India, Australia, and Canada (see **Appendix 1** for full list of cities). Our analyses focused on users within the United States as they make for the bulk of the data. We included only data from heterosexual relationships (i.e., a user who self-identified as male, who expressed interest in females) which reflect the majority of Hinge users.

Sample Description

A user profile on Hinge has data that is pulled from social media (Facebook), entered by the user, inferred from the device used, or generated as a byproduct of the interaction within the app. Data fields include name, gender, age, education, height, and various other basic biographical information. Users are not required to complete all possible fields. Data such as height, education, and religious beliefs may be left blank. Ethnicity was selected by the user upon subscribing to Hinge. We only used ethnicity data in the context of name/initials similarity analysis, per Hinge's request. Fields such as age, name, gender, education, number of social media connections and device type are populated automatically.

To estimate preference and likelihood of effective matching we excluded any users who, for a particular query, did not provide the specific data (e.g., only those who provided their religion were included in queries related to religion). We did not impute missing data given that this would require accessing individual user information rather than aggregated data, which we did not have access to. Additionally, we suspect that in the context of online dating, missing data may be indicative of a deliberate choice not to include the information (i.e., a short man deciding not to disclose his height, thinking this may increase his dating prospects) and therefore should not be altered. More so, when a user is selected based on missing information this in itself may be indicative of a preference. Imputing the data and drawing conclusions based on this may alter the determinations. Accordingly, our sample fluctuated in size depending on the queries used. Nonetheless, we were always working with hundreds of millions of entries.

In prior studies (i.e., Hitsch et al., 2005) populations of online dating participants were compared to general population statistics provided from surveys. These prior studies suggested that the percentage of men is disproportionately represented in the data. In our dataset, albeit slightly skewed toward men, the numbers were virtually the same. A possible match would not be affected by the number of options presented as users are faced with a limited set of users to choose from within a given day. This daily limit is determined dynamically from a combination of available pool size and the user's level of activity. The pool ranges between 10 and 21 per day. Hinge's value proposition at the time of the analyses emphasized trying to initially connect people who had Facebook friends in common but was not limited to this group.

Some concerns exist with regards to the accuracy of user data (Brym and Lenton, 2001; Madden and Lenhart, 2006) as users may misrepresent some attributes. In fact, based on a study by Toma et al. (2008) users indeed misrepresent their height, but not to a significant degree (about half an inch for men). To test for this bias we compared average male and female user heights to national averages in the United States (Fryar et al., 2012). Both male and female users on Hinge were, on average, slightly taller than the national averages (males: 71.1′ compared to national average of 69.3′, $p < 10^{-3}$, t-test, Cohen's D: 0.88; females: 65.3 inches compared to national average of 63.8 inches, $p < 10^{-3}$, t-test, Cohen's D: 0.77). This difference can be partially explained by exceptionally short users who may not declare their height and, therefore, are not represented in our queries. These differences, in conjunction with some users' intentional misrepresentation of their height, would sway the averages slightly. However, since people match based on the provided information, regardless of whether it is true, we treated the height values as if they were accurate. With regard to age and gender, since data is pulled from Facebook, a user must be willing to go through the arduous process of changing their date of birth or gender on Facebook (including waiting for the information to update on the Facebook platform and then repopulating Hinge) in order for those to be represented differently. Although it is possible to do so, it seems unlikely that this would be a common occurrence.

Queries and Analysis Tools

Data were pulled from the Hinge Database using a series of SQL queries, into large Tab-Separated-Value files. All user data were anonymized prior to the scientific inquiry. The academic members of the team had no access to the users' personal information. All data usage was done in alignment with the Hinge license agreement[1]. Ethical review and approval were not required for the study on human participants in accordance with the local legislation and institutional requirements. No personal user communication was read or used in the study, and the only content that was observed—the exchange of contact information—was extracted using a regular expression that indicated whether such information was exchanged (yes/no). No text, user names, or pictures were available to the research team throughout the analyses.

Typical App Record Entry

To open an account on Hinge, users begin by downloading the mobile app to their smartphone. Once they open the app users are prompted to create an account using their Facebook credentials. The user provides Hinge with access to basic information and images. These include name, gender, age, location, occupation, education, etc. (see **Table 1** for a full list of fields).

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[1] https://hinge.co/terms

TABLE 1 | Fields used by the Hinge application for user analysis.

Field name	Example	Populated from
Name (first and last)	Moran C.	Facebook
Gender (male, female)	Male	Facebook
Date of birth	March 14, 1980	Facebook
Current city	Boston, MA	User selection in app
Ethnicity (American Indian, East Asian, Middle Eastern, South Asian, Black/African Descent, Hispanic/Latino, Pacific Islander, White/Caucasian, Other)	White/Caucasian	User selection in app
Hometown	New York, NY	Facebook
Current occupation and position	Professor	Facebook
Education (high school, college, university, graduate school)	Graduate school	Facebook
Number of social medial connections	2,900	Facebook
Number of connections within the Hinge app	100	App
List of Facebook 'likes'	*None*	Facebook
Gender(s) of interest (male, female, both)	Women	User selection in app
Relationship options they desire (casual, dating, relationship)	Relationship	User selection in app
Height	6′2′′	User selection in app
Religious affiliation	Agnostic	User selection in app
About me (short bio)	'I am left handed.'	User entry (300-character limit)
Device type (iPhone, Android)	Android	Device
Mobile OS version	4.2	Device
Timestamp of each action	1480330983	Device

Example of fields for an individual user. Data is populated from the information user enters into the Hinge application and from their Facebook profile. All fields in black are mandatory. Entries appearing in blue are optional fields that may or may not be completed. Entries in red are populated by the device per user and action (i.e., the rating of an individual by the user). A table is maintained per user that includes the list of all individuals rated by a user and the selection for that individual.

Out of all users included in this study, 10% had all fields filled out, 61% did not have height filled out, 82% did not have "open to" filled out ("open to" indicates the type of relationship the user is interested in), 9% did not have education filled out, and 18% did not have a hometown filled out. To complete the registration processes users' photos are pulled from their Facebook account. These photos can be reordered, replaced, or removed.

Once the initial account setup is complete, users are presented with a daily stack of potential matches for review. As part of standard operations, Hinge tracks additional data on the choices and the devices used to make the selections (in red in **Table 1**).

Typical User Experience

A typical experience with Hinge involves a user opening the app using their smartphone and seeing their stack of potential matches. A match is reflected in the form of an image that a user is asked to swipe with their fingers. Swiping an image to the left indicates "no-interest," whereas swiping to the right indicates a desire to communicate with the person further. A match is defined by both users, independently and asynchronously, selecting the respective partner as someone they seek further communication with. If a user matches with another user, they unlock a chat feature of the app. Once the stack of potential matches is complete, the user can wait until the stack is refilled (up to a day) while chatting with users who already matched with them.

Not all information about a potential match is readily available at first glance. Access to religious beliefs, relationship type interest, height, hometown, and a brief bio (comprised of up to 300 characters; 106.4 ± 81.1; mean ± SD) require a user to scroll down.

Not all matches lead to conversations. Even fewer lead to an exchange of a telephone number or other means of communication outside the app.

For the purposes of this study we tracked three characteristics relative to each variable we tested:

Potential Match

The count of every potential couple that *could* occur. Included in this group are both: (1) matches where one user saw another user and rejected them (note that in this case Hinge will not display the choice to the second user since a match cannot occur unless both users respond positively), and (2) matches where one user selected the other, and the second one had the opportunity to select/reject the first user (regardless of whether they selected them).

Conversations

Given that not all matches result in conversation, we define a conversation as an interaction where each person messages the other twice (i.e., Alice messages Bob once. Bob then responds. Alice messages again, and then Bob responds again). This is termed a "four way" by the online dating industry. For the purposes of this paper, any communication less than that is deemed "not a conversation".[2]

Effective Match

Since we cannot track a user's behavior once they leave the app, we consider the exchange of means of communication outside the app as the metric of success (i.e., a phone number exchange). This suggests that both users are interested enough in one another to continue talking and potentially meeting in person. This also suggests that a level of comfort and perceived safety has been achieved to advance the communication to the level of more identifiable information. From this we define the Effective Match Rate (EMR) as the percentage of effective matches relative to the total number of potential matches.

Social Ratio Metric

To compare psychological attributes, we used standard popular metrics of personality (Little, 2014). One such measure is introversion. As we cannot judge directly if a person is introverted or extroverted, we used a user's Facebook friend count as a proxy. This is based on the fact that introverted individuals are likely to have fewer friends relative to the average number of friends in their peer group (Amichai Hamburger and Vinitzky, 2010). When examining an average user's friend count, we found that the numbers vary based on the city a person lives in, their gender, and their age. For example, Hinge users who are older women have far fewer Facebook friends than younger women (on average, a 45-year-old woman has 360 fewer friends than a 25-year-old woman). For this reason, we evaluated each user in comparison to others of the same age, gender, and city.

A user's "Social ratio" is defined as the ratio between the number of Facebook friends they have and the average number of Facebook friends that users of the same age, gender, and city have. Users who have a Social Ratio lower than 1 veer toward introversion while those who have a Social Ratio above 1 veer toward extroversion.

Education-Related Data

To evaluate the effects of school ranking, liberal arts education, and NCAA conference participation, we matched the Hinge/Facebook school entries to those of the Integrated Postsecondary Education Data System (IPEDS) database. These were then used to map users' schools to National Center for Education Statistics, which allowed for binning based on academic similarity (test scores, school's focus disciplines, etc.).

Not all schools listed in the Hinge database were found in the IPEDS database. Some schools are not accredited and would not be included in IPEDS. In other cases, users misspelled their school names or simply made up fake schools (e.g., "The School of Hardknocks"). Schools outside of the ones recognized were treated as missing data. Eighty one percent of users in the sample attended the same 1,500 schools.

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[2] The rationale behind using "four way" as a measure of interest is so that the criteria for effective matching will reflect an actual likely desire to interact. Given that the cost of swiping right on multiple profiles on mobile dating apps is low—allowing users to do so without the necessary need to effectively choose a partner—some users use strategies of selection that only start the evaluation process *after* both parties have expressed interest. Therefore, if one party realizes that they are not interested then they will not initiate a conversation. So, if both people initiated a conversation and responded to the other person's communication, the mobile dating industry considers the communication effective.

For categorization of colleges by institution type (Liberal Arts College or National University) we looked at the rankings (U. S. News and World Report, 2016) of the top 200 schools by institution type.

For categorization of colleges by Division 1 NCAA sports conferences, we compared the IPEDS database to online listings of school participation (see **Appendix 2** for breakdown). As Ivy League is an NCAA conference designation, we also used these data to define Ivy League schools.

RESULTS

To examine the ways Hinge users pair into a relationship we looked at data from 421,690,471 potential matches. These reflect data from over one million users, with an equal distribution of men/women. Before users can chat and exchange contact information, they need to review one another's profiles. To estimate whether users were swiping based on the readily available information in a profile (i.e., the image) or whether they were viewing additional information in an extended profile, we looked at the average time spent scanning the candidate. Men engaged with the profile for 6.7 ± 4.7 s. Female users spent significantly more time making their choices (11.1 ± 6.9 s; $p < 10^{-3}$, *t*-test. Cohen's D: 0.82).

The time spent viewing profiles suggests that most of the selection occurs based on immediately available cues such as aesthetics, visual presentation, and basic notable information that is readily accessible (i.e., occupation or mutual friends). Given that the estimated average time it takes to saccade to an item on an average screen size is about 200 ms (Mackay et al., 2012), we estimate that a typical user had up to 33 pieces of information that they were able to capture before making a decision. Face recognition assessment, emotion assessment, and attraction preferences require 1–5 s to process (Todorov and Uleman, 2002; Willis and Todorov, 2006; Todorov et al., 2009; Venkatraman et al., 2015) leaving the male user anywhere from 1.7 to 5.7 s to incorporate most of the textual information into a decision. Female users would have 5.1–10.1 s to incorporate the additional information. This is sufficient to typically read 2–4 fields while also scrolling through the profile page (Dyson and Haselgrove, 2001).

Given that faces are likely to draw the users' attention first, followed by the text (Milosavljevic and Cerf, 2008; Cerf et al., 2009), we suspect that visual information was processed for a longer time during the decision. In order to generate our own baseline assessment and not rely solely on prior works, we also ran a query on user rating data to determine the typical scan time for a profile. Response times were measured as seconds elapsed between the previous rating and the current rating time. These baseline estimations included 1,000 randomly selected users (500 males and 500 females). The average scan time in our data was 700 ms longer than the literature standard, with an average of 7 s allotted to a profile. This is enough time to load and review all the personal information on the user's front page. Although male users spend less time per profile, they engage with more profiles, leading to similar amounts of total time spent reviewing potential matches as female users do.

The likelihood that any two potential matches would have a conversation is 0.51%. This is the total number of "four way" conversations (2,148,947) divided by all potential matches across the entire database. The average EMR across the entire dataset is 0.12% (508,989 effective matches divided by all potential matches). This means that for every 4.23 people that a user chats with, they will exchange contact information with one. In comparison, work that created dummy Tinder profiles and measured how many of them were selected, shows that roughly 0.6% of males who select a female get selected by her (or 1 out of every 167), and that 10.5% of females who select a male get selected by him (or about 1 out of every 95) (Tyson et al., 2016). This means that, on average, men say "yes" to 17.5 times as many women than women do men.

It is worth noting that given the size of our dataset, even small effects are significant. That is, even a change of fractions of a percent in EMR is likely to be significant and meaningful. We therefore used Cohen's D as an additional metric to quantify the effect size when necessary. We used a cutoff of 0.8 to note large effects and 0.2 to note small effects throughout.

Below we characterize a number of individual attributes and their effect on the matching likelihood:

Education

While one might think that the choice of partner in a rapid binary selection processes is skewed toward more superficial properties—typically aesthetics—we tested the correlation between cognitive and more long-term aspects of the match and their effect on the outcome. One such aspect is education. A typical higher education in the United States lasts 4 years. The selection of school reflects a choice of location, socio-economic status, intellectual goals/abilities, and also, at times, shared values (e.g., a choice to go to a small liberal arts college trades size of student body for type of education. Alternatively, attending a competitive technology-based institute of higher education may have a notable difference in ratio between men and women).

These preferences, tradeoffs, and considerations reflect a person's perspective and values and can thereby also influence their preferences in dating. To gain insight into these characteristics, we evaluated the influence of university type on effective matching. Specifically, we examined the designations of schools (Liberal Arts and Ivy League) and the school's participation in an NCAA conference on EMR.

The Influence of Attending a Liberal Arts College (LAC) on Effective Matching

Liberal arts colleges attempt to impart students with a well-rounded education in the arts and sciences (Grove, 2015). They focus on developing intellectual capacities and broad knowledge. These colleges tend to be smaller. For the purposes of this research we compared schools ranked by the U.S. News and World Report (USNWR) in the LAC category with top-ranked National Universities and with colleges not present in the rankings.

When both men and women attended a liberal arts college their EMR was 0.20%, a 38.0% increase compared to cases where only one attended an LAC and the other attended a ranked non-LAC. Similarly, attendees of LACs were 34.6% more likely (0.20% EMR versus 0.15%) to match with each other than with people from unranked schools. Among users who both attended a non-LAC ranked by USNWR, the EMR was 0.17%. This is higher than people from unranked schools matching with each other and people from ranked non-LAC matching with people from unranked schools, both having an EMR of 0.16% (see **Table 2**).

The Influence of Attending an Ivy League College on Effective Matching

In the United States, the prestige of attending an Ivy League college is paramount to many other academic markers of success, as it has implications on social status, future career, and potential earnings (Rivera, 2011). With so much value placed on attending these institutes, we asked whether attendees of these schools select one another and match more effectively with one another.

When both users attended an Ivy League school, they had an EMR of 0.27%. This is more than double the average EMR of 0.12% and is 64.3% more frequent than if only one person attended an Ivy League school and the other person attended any other institute of higher education (0.27 vs. 0.17%; see **Table 3**).

NCAA Sports Conferences Affiliation as It Relates to Effective Matching

As users did not directly state if they had sporting allegiances, we reviewed the NCAA conference their college participated in as a proxy for such preference. In situations where two users attended schools that participate in the same NCAA conference, there was a positive increase in probability of effective matching versus situations where the users had dissimilar conferences. The increase ranged from as little as 7% for those students from “Big Ten Conference” schools to as much as 91% for students from the “West Coast Conference.” On average, the probability of effective matching increased by 21.1% if both users shared such affiliation (see **Table 4**).

Given their small sample size, we excluded from the list conferences with attendance below 50,000 people (see **Appendix 3** for list of school excluded). We note that similarity in sports allegiance may simply mean that the two users are, in fact, in the same school, but an overwhelming percentage of Hinge users are already graduates of college suggesting that, unless they stayed in the same city where their university was, they are likely being presented with a wider variety of people.

Mobile Device Type as It Applies to Effective Match Rate

It has become a common phenomenon for consumers to align themselves with brands that they love and use (Allison and Uhl, 1964; Kressmann et al., 2006; Tuškej et al., 2013). These brand allegiances can have subtle impacts on the way people behave and

TABLE 2 | Liberal arts college.

College	Total possible matches	Conversations	Effective matches	Conversation probability	EMR
Both went to LAC	329,003	2,652	674	0.81%	0.20%
LAC vs. non-LAC ranked	3,588,852	22,174	5,326	0.62%	0.15%
Both LAC vs. different ranked				**30.5%**	**38.0%**
LAC vs. non-LAC unranked	8,893,225	56,275	13,536	0.63%	0.15%
Both LAC vs. different ranked				**27.4%**	**34.6%**
Both non-LAC ranked	12,872,132	86,337	21,553	0.67%	0.17%
Both non-LAC ranked vs. different ranked				**8.6%**	**12.8%**
Both Unranked	80,304,037	535,216	130,100	0.67%	0.16%
Unranked vs. ranked	69,598,483	452,860	112,092	0.65%	0.16%
Both unranked vs. ranked				**2.4%**	**0.6%**
Overall	166,692,507	1,099,239	269,745	**0.66%**	**0.16%**

TABLE 3 | Ivy League colleges.

Ivy league	Total possible matches	Conversations	Effective matches	Conversation probability %	EMR %
Both Ivy league	105,390	911	289	0.86	0.27
Ivy vs. non-Ivy	6,223,089	38,728	10,388	0.62	0.17
Same vs. different				38.9	64.3

TABLE 4 | NCAA sports conferences.

NCAA conference	Increase in probability of effective match %	Significance (*p-value*)
Northeast Conference	152	0.003
Metro Atlantic Athletic Conference	147	10^{-4}
Ohio Valley Conference	121	0.004
West Coast Conference	91	0.001
Conference USA	84	0.007
Southeastern Conference	74	10^{-4}
Mid-American Conference	70	0.003
Ivy League	64	10^{-4}
Atlantic 10 Conference	59	10^{-4}
Southland Conference	58	0.099
American Athletic Conference	58	10^{-4}
Missouri Valley Conference	50	n.s.
Patriot League	37	0.004
Big West Conference	34	0.036
Sun Belt Conference	33	n.s.
Mountain West Conference	28	n.s.
Big 12 Conference	25	0.003
Atlantic Coast Conference	20	0.006
Colonial Athletic Association	17	0.046
Pac-12 Conference	15	10^{-4}
Big Ten Conference	7	0.028
Big East Conference	2	n.s
Southern Conference	−2	n.s

the choices they make (Barnett and Cerf, 2015). These brands are also shown to reflect and correlate with personality types and characteristics (Grant, 2017). Our dataset included the mobile operating system each user was using (iPhone or Android). We tested whether there is a relationship between dating preferences and operating system selection (see **Table 5**).

The data suggests that users who have the same smartphone (both iPhone or both Android) experience an increase of 8.9% in effective matches versus users with dissimilar phones, although the knowledge about the operating system used by the other user is not overtly accessible. Android users had an EMR of 0.13% (a 14.14% increase over mixed), followed by iPhone users who had an EMR of 0.12%. Users who had dissimilar phones had an EMR of 0.11%. The differences between all device types were significant ($p < 10^{-3}$, t-test).

User Initials as They Correlate With Effective Matching

One popular scientific claim known as "implicit egotism" suggests that similarity to oneself generates appeal/attraction in the context of names that resemble one another (Pelham et al., 2002; Jones et al., 2004). One finding from this line of research suggests that people who have the same initials (i.e., Mark Goffman and Maya Goffer) are 8.8% more likely to marry one another than those with differing initials (Jones et al., 2004). Whereas the original research was conducted on a dataset of 14,534 people, we now have data from over 421 million potential matches, so we tested the results in a more robust way. User names on Hinge appear as the complete first name and the first initial of the last name (i.e., Albert E.). Users with the same initials had, on average, an 11.3% increase in effective matching compared to those with dissimilar initials (0.13% versus 0.12%; $p < 10^{-3}$, t-test; **Table 6**). While implicit egotism has been controversial in the literature and the effect size is small, our dataset allows for a testing and verification of the hypothesis. Our results hold upon controlling for religious affiliation, which could have been a driver of disproportionate name selection (i.e., some religion have preference for some names that may increase their proportion in the dataset).

Desired Relationship Type as It Relates to Effective Matching

Common assumption pertaining to users of dating apps who select potential partners based on little preliminary information is that they are likely to pursue casual romantic relationships. Although we have no data on the nature of the relationship once the users exchanged phone numbers, many users will disclose the type of relationships they desire within the app. Users can select none, one, two or all of the following three options: "Casual," "Dating," or "Relationship." Users whose relationship intentions are aligned have an increased rate of effective matching (**Table 7**). When both users state they desire a "Relationship" (understood as a committed relationship) their EMR is 0.20% compared to only 0.13% when only one user states a desire for a relationship. Similarly, when both state an interest in "Dating" the EMR is 0.19% compared to 0.14% when only one person expresses an interest in dating. Those users who are both looking to be "Casual" have an effective matching rate of 0.15%, which is lower than when both are looking

TABLE 5 | Mobile device type.

Device	Total possible matches	Conversations	Effective matches	Conversation probability %	EMR %
iOS/iOS	298,215,755	1,574,075	370,053	0.53	0.12
Mixed: 1 Android and 1 iOS	98,290,340	461,698	112,187	0.47	0.11
Android/Android	8,280,795	41,583	10,788	0.50	0.13
Users have same phone	306,496,550	1,615,658	380,841	0.53	0.12
iOS/iOS vs. mixed				12	8.72
Android/Android vs. Mixed				7	14.14
Same vs. different				**12.2%**	**8.9%**

TABLE 6 | User initials.

Condition	Compatibility count	Conversations	Effective matches	Conversation probability	Effective match probability
Identical Initials	1,736,588	9,575	2,332	0.55%	0.13%
Differing Initials	419,807,709	2,138,336	506,439	0.51%	0.12%

TABLE 7 | Desired relationship type.

Conditions	Total possible matches	Conversations	Effective matches	Conversation probability %	EMR %
Both interested in "Causal" relationship	1,487,847	10,565	2,277	0.71	0.15
Male Casual, Female not	38,410,837	223,604	50,628	0.58	0.13
Female Casual, Male not	11,613,164	62,372	13,565	0.54	0.12
Casual vs. non-Casual	50,024,001	285,976	64,193	0.57	0.13
Both interested in "Dating"	17,194,118	122,238	32,763	0.71	0.19
Male Dating, Female not	61,745,450	336,695	81,824	0.55	0.13
Female Dating, Male not	65,375,580	373,637	91,728	0.57	0.14
Dating vs. non-Dating	127,121,030	710,332	173,552	0.56	0.14
Both interested in "Relationship"	17,078,132	124,039	34,251	0.73	0.20
Male Relationship, Female not	58,210,924	312,425	76,751	0.54	0.13
Female Relationship, Male not	67,451,437	392,506	97,711	0.58	0.14
Relationship vs. non-Relationship	125,662,361	704,931	174,462	0.56	0.14

for a "Relationship" and both are looking for "Dating" but still higher than the 0.13% EMR when only one person states an interest in being "Casual." All differences are significant ($p < 10^{-3}$, t-test). Note that there are overlaps within the mixed options (i.e., "Dating" and "something else" could end up being the same as "Casual" and "something else," if in this example the "something else" ends up being "Dating" or "Casual"). Therefore, comparison between the mixed options were not complete.

In both the cases of "Dating" and "Relationship" women more often match with men who have dissimilar interests (0.14% EMR) than men who match with women of dissimilar interests (0.13% EMR; $p < 10^{-3}$, t-test). In the case of the choice of "Casual" the opposite is happening: men who are looking to be "Casual" and women who are not have an EMR of 0.13% versus women who want to be "Casual" and men who do not (0.12% EMR; $p < 10^{-3}$, t-test).

Religious Belief in Comparison to Effective Matching

Religious belief has been a long-standing point of contention for couples getting together (Blackwell and Lichter, 2004; Mahoney, 2005; Hitsch et al., 2010). Conversely, common religious affiliation can increase the chances of shared values and interests. In an era where we see a growing departure from faith, one may ask how important is it for couples to share the same religion?

People who either do not list their religion or have no religious affiliation make for a large pool of potential matches. However, looking at the data from users who state their religious affiliations, we see that users who share the same religion have an average 97.5% increase in their EMR (to 0.21%) compared to people with mixed religions (0.11%; **Table 8**). Chances of effective matching for two people of the same religion is as high as 0.94% for Muslims (856.5% chance over Muslims and non-Muslim) or as low as 0.17% for Catholics (50.0% chance over Catholics and non-Catholics). The smaller the community representation in the data, the more likely they were to effectively match with people of the same religion. Hindus make for only 327,911 potential matches in our dataset and have 0.61% EMR. Similarly, Muslims make for only 3,741 potential matches with 0.94% EMR. In contrast, Christians have 8,558,535 potential matches and 0.20% EMR and Jews have 8,026,793 potential matches with 0.30% EMR. Notably, these numbers are not proportional to the numbers in the larger population but are aligned with census data of younger app users, primarily in urban environments. Our dataset does span a wide range of cities and locales and, accordingly, reflects a representative offering of religions and political views.

For all religious affiliations, except for Judaism, women of a particular religion had an EMR of 0.13% with men outside their religion. Non-Jewish women were 5.7% more likely to match effectively with men outside their religion than their male counterparts. Jewish women and non-Jewish men had a low EMR of 0.09% (significantly different than the 0.30% Jewish women-men pairing; $p < 10^{-3}$, t-test).

Introverts and Extroverts

Western cultures tend to emphasize outgoing or extroverted personalities (Allik and McCrae, 2004; McCrae and Terracciano, 2005). The general tendency that is often aligned with extroversion suggests that extroverts gain energy from engaging with others, whereas introverts prefer more intimate social interactions (Amichai Hamburger and Vinitzky, 2010). We investigated whether users match most effectively with others who share their level of introversion/extroversion.

TABLE 8 | Religious beliefs.

Religion	Total possible matches	Conversations	Effective matches	Conversation probability %	EMR %
Both Catholic	7,000,149	49,750	11,960	0.71	0.17
Male Catholic, Female not	37,098,926	183,370	41,955	0.49	0.11
Female Catholic, Male not	43,902,466	218,159	50,334	0.50	0.11
Catholic vs. non-Catholic	81,001,392	401,529	92,289	0.50	0.11
Both Christian	8,558,535	69,302	17,231	0.81	0.20
Male Christian, Female not	32,553,015	160,043	37,282	0.49	0.11
Female Christian, Male not	47,126,801	232,754	54,875	0.49	0.12
Christian vs. non-Christian	79,679,816	392,797	92,157	0.49	0.12
Both Hindu	327,911	7,172	1,988	2.19	0.61
Male Hindu, Female not	4,234,491	16,401	4,471	0.39	0.11
Female Hindu, Male not	3,968,157	20,874	5,413	0.53	0.14
Hindu vs. non-Hindu	8,202,648	37,275	9,884	0.45	0.12
Both Jewish	8,026,793	83,604	24,237	1.04	0.30
Male Jewish, Female not	31,322,221	136,600	34,314	0.44	0.11
Female Jewish, Male not	37,413,003	151,240	34,261	0.40	0.09
Jewish vs. non-Jewish	68,735,224	287,840	68,575	0.42	0.10
Both Muslim	3,741	138	35	3.69	0.94
Male Muslim, Female not	890,443	3,511	805	0.39	0.09
Female Muslim, Male not	738,226	3,437	788	0.47	0.11
Muslim vs. non-Muslim	1,628,669	6,948	1,593	0.43	0.10
Both Spiritual	1,501,120	11,747	3,817	0.78	0.25
Male Spiritual, Female not	15,831,114	81,991	22,144	0.52	0.14
Female Spiritual, Male not	19,681,091	116,478	32,240	0.59	0.16
Spiritual vs. non-Spiritual	35,512,205	198,469	54,384	0.56	0.15
Both Agnostic	1,630,120	10,169	2,977	0.62	0.18
Male Agonistic, Female not	25,140,010	117,015	30,036	0.47	0.12
Female Agonistic, Male not	16,474,358	83,530	21,388	0.51	0.13
Agnostic vs. non-Agnostic	41,614,368	200,545	51,424	0.48	0.12
Both Atheist	567,176	3,937	999	0.69	0.18
Male Atheist, Female not	16,927,835	76,374	17,883	0.45	0.11
Female Atheist, Male not	7,934,231	37,146	8,889	0.47	0.11
Atheist vs. non-Atheist	24,862,066	113,520	26,772	0.46	0.11
Both Other	368,060	2,084	566	0.57	0.15
Male Other, Female not	13,950,519	70,846	17,183	0.51	0.12
Female Other, Male not	7,728,977	38,670	10,011	0.50	0.13
Other vs. non-Other	21,679,496	109,516	27,194	0.51	0.13
Total same choice	**21,427,114**	**185,449**	**48,645**	**0.87%**	**0.23%**
Total difference choice	**400,175,176**	**1,962,256**	**459,933**	**0.49%**	**0.11%**

In our dataset, introverts rarely match effectively with other introverts, but when at least one member of a potential match is an extrovert the EMR rises significantly (**Figure 1**). Men who have a social ratio of 2 and above (that is, they have twice as many friends as the average) are significantly more likely to effectively match with women of every level of the extroversion-introversion spectrum. This effect increases with men's social ratio.

Effective match rates increase with social ratios for both genders. These effects are stronger when women have a social ratio above 2. These women had an EMR 53.8% higher than women with a social ratio below 2 ($p < 10^{-3}$, sign-test). These effects are amplified disproportionately when men's social ratios are also above 2. For example, men's EMR increased by 71.9% when their social ratio was above two compared to below 2. When men's social ratio was four times higher than the average their EMR increased by 157.5%.

Height

Height has been shown to have an impact on multiple facets of dating choices. The literature suggests that taller men have a higher chance of generating initial interest among women, that heterosexual couples where men are several inches taller than women are happier, and that shorter men are likely to marry later in life (Weitzman and Conley, 2014; Sohn, 2015). Our analysis uncovered a more complex relationship between men's and women's heights. When examining which height combinations have the highest EMR we found that optimal selections are dependent on a combination of gender and height (**Figure 2**).

Effective Match Rate (function of male height m and female height f) is:

$$EMR(f,\ m) = \sum_{i=0}^{2}\sum_{j=0}^{2} a_{ij} f^i m^j$$

where $a_{ij} = \begin{pmatrix} 3,172 & -90.01 & 0.64 \\ -99.49 & 2.83 & -0.02 \\ 0.78 & -0.02 & 0 \end{pmatrix}$

Notice that the coefficient matrix is nearly symmetric with a minor weighted influence toward female heights.

Accordingly, the optimum female height for a male user (function of male height m):

$$EMR^{'}(m) = -\frac{1}{2}\cdot\frac{\sum_{i=0}^{2} a_{1i} m^i}{\sum_{i=0}^{2} a_{2i} m^i}$$

And the optimum male height for a female user (function of female height f):

$$EMR^{'}(f) = -\frac{1}{2}\cdot\frac{\sum_{i=0}^{2} a_{i1} f^i}{\sum_{i=0}^{2} a_{i2} f^i}$$

The optimum women heights for matching with men of any height are in the range $5'1''$–$5'6''$ (66.7% of the female population in their 20 s).

DECISION MAKING PROCESS

While men and women must both select each other in order for an effective match to occur, their strategies of selecting a partner may differ. Our results show that individuals who share common attributes (religion, education, etc.) are likely to match effectively at the end of the courtship journey. To address the decision making process in full, we further investigated the initial stage of the matching journey.

Presumably, users can identify partners who share traits with them early on or start with a wider net of options and converge to traits similar to theirs. That is, users can either be very selective in the initial choice or accept many possible matches and hope that among the numerous options there are also partners who are similar to them.

Strategies of selection can be attributed to a specific preference or to lack of certainty about the choice and the hope that additional information will increase the information. Similarly, strategies of rejection can be attributed to lack of interest, the elimination of highly appealing options due to a feeling that the person is "out of one's league," or as a preventive measure to avoid future rejection when they do not match.

Given that at the end of the match process people effectively matched with others who largely shared traits with them, we investigated whether men and women also exhibit similar strategies in the early stage of the matching processes. That is, are the similarities in outcomes the consequence of similarity in early choice strategy, or a gradual convergence?

To investigate the early binary choice, we tried to fit the decision using classical prediction model. Whereas most decision making models (i.e., the Drift Diffusion Model) typically estimate the "response time" and the "accuracy" (Fehr and Rangel, 2011) of a decision, we replaced the "accuracy" with "consistency" (in the absence of "ground truth" for individuals, we measured how likely a user is to agree with the selection of prior control group users). We fitted men/women's choices and looked at their similarities in time, consistency, and other attributes that can be inferred from Drift Diffusion Models (DDM).

To test similarities in decision making we asked the following questions: (1) Do users tend to be similar in their preferences early in the choice process? That is, do men/women first choose the same people or do idiosyncrasies arise in preliminary selection? (2) Do men/women spend similar time on the early choices, or are there differences in the early stages that potentially shed light on the alternative trajectories in their thought processes? (3) Do users exhibit "streaks" of consistently saying "yes" (or "no")? This would suggest a less focused search method, and that the ultimate similarity in effective matches are adopted while the individuals converse or after they have learned that there was an initial mutual desire to interact.

To estimate consistency, we assigned a likelihood to be selected (0–10) to 100,000 randomly selected users (5,000 men), who were seen by at least 200 people. We calculated the likelihood by looking at the chance of a person being selected by people who previously viewed them. Simply, if a user was seen by 100

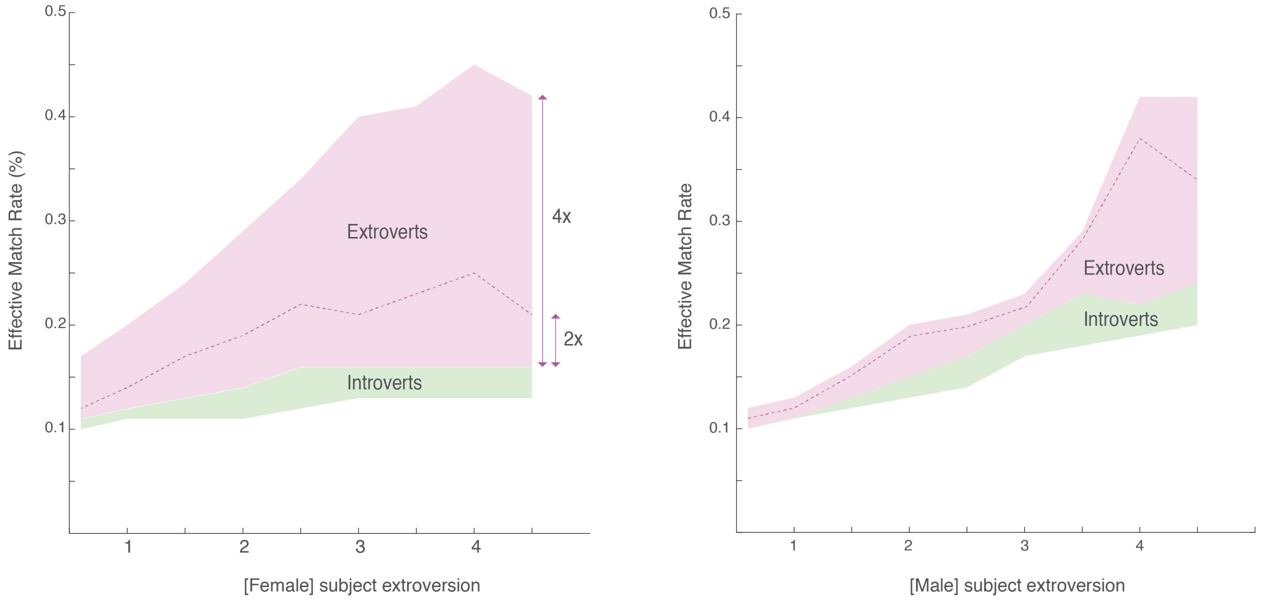

FIGURE 1 | Effective Match Rate as it relates to female **(left)** and male **(right)** social ratio. Female/Male extroversion level (measured in number of times above the average number of Facebook friends for their city, age, and gender) and their likelihood of finding a match. Men whose social ratios are four times more than the average, for example, are likely to have a higher EMR with women whose social ratio is three times above the average. The top right points and bottom left points are identical since they reflect the extreme matching of both genders.

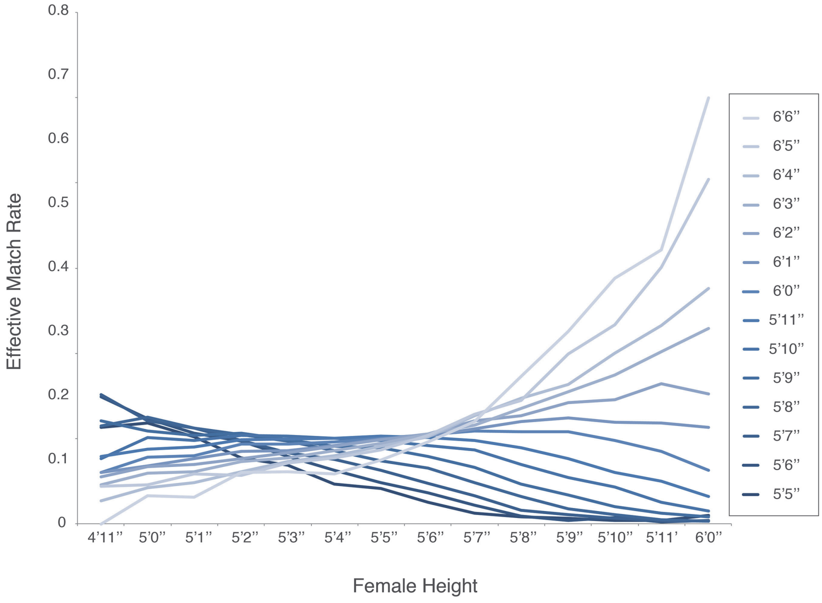

FIGURE 2 | Effective match rate as it relates to a female height (from 4′11′′ to 6′0′′) and male height (5′5′′ to 6′6′′).

individuals and was selected 20 times, we would score the person's desirability as 2.

When testing for the consistency of a user's selections, we evaluated how much a choice aligns with those of prior viewers. When viewing a candidate whose score was high (i.e., 9), the expectation is that a new viewer would select them as well. Similarly, a user whose score is 1 was likely to be rejected. When a new user rejects a 9 or selects a 1, they are inconsistent with prior viewers and reflect a unique view. We analyzed only those extreme cases: users whose score was above 8 or below 2 (see **Figure 3**). Users whose scores were closer to the middle (i.e., 5) suggest an idiosyncratic evaluation by viewers. Excluding these users biases our estimates toward higher consistency, in alignment with prior works showing that

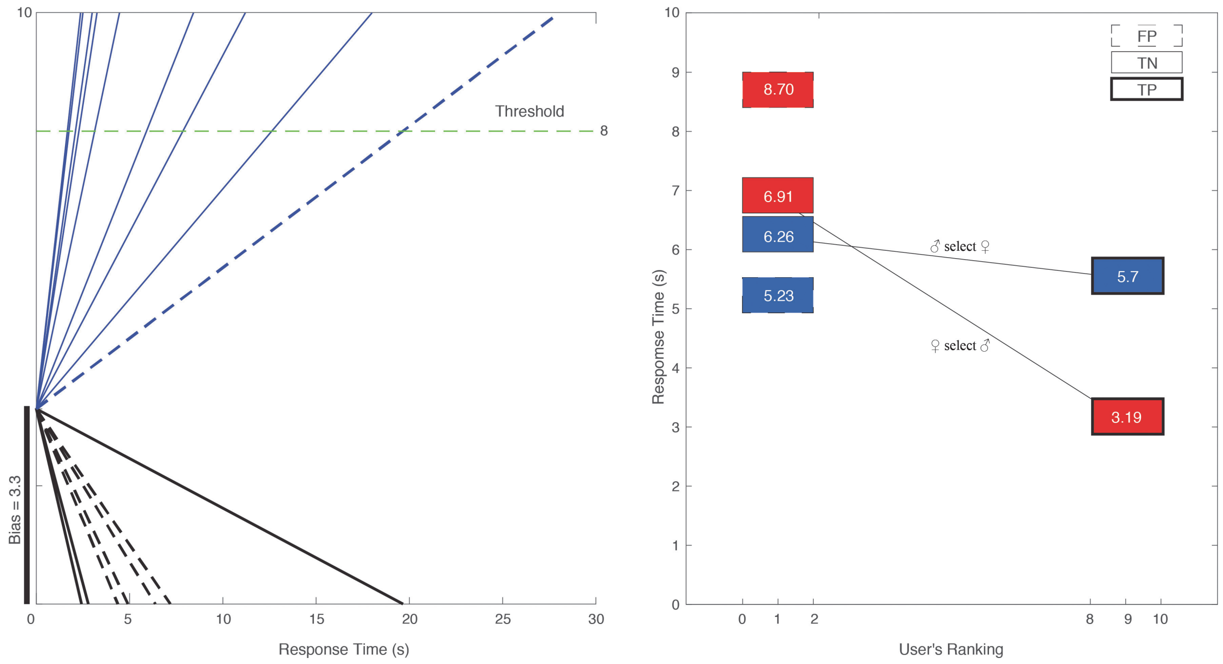

FIGURE 3 | (Left) A male user's partner selection modeled through DDM. We show (*x*-axis) the time the user took to make a selection when faced with candidate profiles. The user selected multiple women whose rank was above 8 (blue solid lines) and rejected multiple women whose rank was below 8 (black solid lines). We mark the selection as "True Positive" ("hit") and the rejection of lower ranked women as "True Negative." "Miss" ("False Negative") would be a rejection of a woman ranked above 8 (dashed black lines) and "False Positive" would be the selection of a low-ranked woman (dashed blue line). Based on the user's prior choices we can also estimate his "bias." The user tends to accept 33% of the women he sees. His response time is shorter when selecting a high-ranking woman and rejecting a low-ranking one. **(Right)** Mean response time for men selecting women (blue) and women selecting men (red) who are ranked 8–10 (True Positive; solid bold lined square) or rejecting ones ranked below 2 ("True Negative"; non-bold solid lined squares). Accepting a user that others typically reject ("False Positive") is depicted with dashed lines.

individuals are generally more likely to be consistent in ranking content presented visually (Cerf et al., 2007). This consistency assessment allowed us to learn whether men/women are similar in the way they make their decision.

Figure 3 depicts the trial duration in 17 trials for subject 2 (male) and threshold of 8 (indicating that any individual they see whose score is above 8 is expected by our model to be selected). The subject indeed selected 8 of the choices. He rejected four of the women he was presented with, whose ranks ranged between 1.6 and 1.9 (below the threshold) and accepted one woman who was ranked below the threshold. The response time for the below-threshold acceptance was notably longer (28.03 s). The acceptance of all high-ranking women was much faster, with the highest-ranking woman (ranking 8.9) selected after 4.91 s and the fastest rejection (lowest ranking woman 1.6) after 2.42 s. The subject's personal bias was rather low compared to other men (3.3 on a 0–10 scale, suggesting that a woman whose rank is below 3.3 would normally be rejected by the person). The DDM assumes a random walk and not a linear trend toward the goal, however given that we only know the trajectory based on the final outcome we plot those as straight lines.

Estimating Consistency

Men spend 5.70 ± 0.3 s accepting highly desired women, whereas women spend nearly half the time (3.19 ± 0.8 s) accepting a man who prior women ranked highly (**Figure 3**; $p < 10^{-3}$, *t*-test; Cohen's D: 3.94). While women are faster in selecting the desired men, they are slower in rejecting the undesired ones. Women would spend 6.91 s before rejecting a man that other women ranked 2 or below. Men assessing profiles of undesired women spend 6.26 s on this rejection. In alignment with the DDM we can term the acceptance of a desired person "True Positive" ("hit") and the rejection of an undesired one "True Negative."

False Positive is an acceptance of a person who is ranked below 2. Women take longer to do so (8.7 s) than men (5.2 s). Simply put, women are faster in accepting an attractive man, while men are faster in rejecting an unattractive woman. Altogether, men seem to spend equal time on all profile assessments, whereas women are notably different in assessing desired men from undesired ones.

Subjects occasionally spent an unreasonably long time deciding (e.g., 295 s before a swipe). This could be due to the fact that they looked away from their phone or used the application in a non-typical way. To improve our estimates, we tried removing trials with lengths above the mean + 1 SD. These trials constitute 8.1% of the total. With these trials excluded, all choices decreased in similar proportions and, altogether, show average differences of 1.3 s in all attributes. For example, the average response time for women decreased to 2.1 s when selecting a desired man (drop of 1.09 s). The response time decreased by 1.1 s for the selection of desired women by men. The only notable deviation from the prior results was the rejection of undesired men by women, which decreased to 6.1 and now seems more within the realm of other choices rather than an outlier.

Model Fit

Using our definition of True/False Positives/Negatives we could now fit our data with a DDM to estimate the time to decide and see if men/women seem to employ similar strategies in their initial selection. DDM typically assumes that a choice is binary and has two possible outcomes: select the person (1) or reject the person (0). The normalized range of 0–10 often assumes that the initial state of the selection is at 5, but this is not always the case. One way to assess the initial state is by estimating an individual's likelihood of selecting *an* option regardless of the one faced (e.g., a user that says "yes" to 90% of choices would start at 9 whereas one that says yes to only 40% of the choices would start at 4). We term this initial setting the *bias*. We assessed the *bias* for each individual prior to fitting the model based on at least 50 prior choices they made. Next, we estimated the time a user spent making each choice. Our estimate essentially aligned with the standard DDM equation:

$$dx = \tau dt + \varepsilon \tag{1}$$

where τ is the evidence or information the user has in order to make their choice between the two options at any time point dt (their Threshold for a yes/no), and ε is a noise term. The noise, on average, should integrate to zero.

To estimate the decision making process we looked at a single choice made by each of our 100,000 selected users. Each row corresponds to one selection (i.e., a male user viewing a female user and rejecting her). This yields a table of 100,000 rows with each row having the following four fields: the user's gender (male/female), the rating of the user they were viewing (0–2 or 8–10), the choice they made (accept/reject the user), and the response time for the choice rounded to the nearest integer.

We note that adding a ranking of the selecting user in addition to that of the selected user would have allowed us to add an additional feature to the decision model. However, this would deviate from typical DDM. Therefore, we did not incorporate this information (a study that did focus on the interaction between the attractiveness of the selecting user and the selected user was done by Bruch and Newman (2018).

We randomly selected 70% of the data as a training set for a classifier (Linear Discriminant Analysis classifier, using Matlab's *fitcdiscr* function) while holding out the remaining data for testing. Then, we estimated the response time for each choice of the remaining data based on the gender, target user's rating, and selection. Simply, we tried to predict the time it would take a user to accept/reject another user based on their ranking. This aligns with decision making models that suggest a tradeoff between speed and accuracy (rejecting an unattractive user or accepting an attractive one). We compared our response time predictions to the correct ones and averaged the resubstitution error (ranging from 0 to 1) to get an estimate of our classification accuracy. We repeated this entire process 1,000 times to generate a distribution of accuracies (**Figure 4**).

Our model average prediction accuracy was 59.3%. That is, knowing a user's gender, we can predict the time they would take to accept/reject another user with nearly 60% accuracy, without additional prior knowledge. Adding the *bias* term to the equation increases the accuracy to 61.05%.

Men are 3.09 times more likely to select a desired woman when they respond faster than the average (20.36% compared to women at 6.58%). When looking only at the extreme cases (e.g., acceptance of a person who is ranked below 1) men accept a low-ranking woman (False Positive) 4.18% of the times and women do so 9.42% of the times. However, whereas a man will spend 8.3 s on the selection, women increase their time to 14.20 s. These are significantly higher ($p = 0.01$ for all comparisons, t-test) than all other choices.

Streaks

Finally, we moved from looking at the choice as a single outcome to looking at the choice sequence ("streak") in order to see if there are differences in the strategies that men/women employ when looking at multiple choices. This, in our model, would fit in the bias term as it includes *memory* of prior information in each choice. We focused on the tendency to go on "Mate Binging" when a user essentially accepts/rejects multiple options in a sequence. This typically suggests less attention to each individual choice. It is important to note that the design of the app at the time of the study limited a user to 21 potential matches a day (the exact limit was determined by an algorithm, with an average of 15 matches per day). If a user had a streak, or "binge," of 45 "yes" choices in a row, it would have been completed over at least 3 days.

When examining selection streaks (the number of potential matches that users respond to consecutively with the same response—either all yes or all no) we see an interesting difference in strategy between men and women.

The average longest "yes" streak for women is 46.26 (**Figure 5**). However, few women are likely to go on such a streak of saying yes (1.3%), whereas the majority of women (43.1%) are likely to have their longest streak of saying "no." The average longest "no" streak is 37.02. Men are divided between those whose longest streak is saying "yes" and those whose longest streak is saying "no" nearly equally (26% "yes" and 24% "no"). Men say "no," on average, to 29.9 women consecutively.

Initial Choice Strategy

Taken together, our results suggest differences in strategies between men and women in the initial stages of the choice process across all metrics evaluated. Therefore, one can assume that the narrowing of the choice happens later in the process, after the initial screening has happened. Given the selection strategies we observed, it is likely that users start the choice process by focusing on salient attributes such as visual features and basic observable characteristics (i.e., characteristics that suggest similarity in taste). We implicitly rely on the convergence of women being more

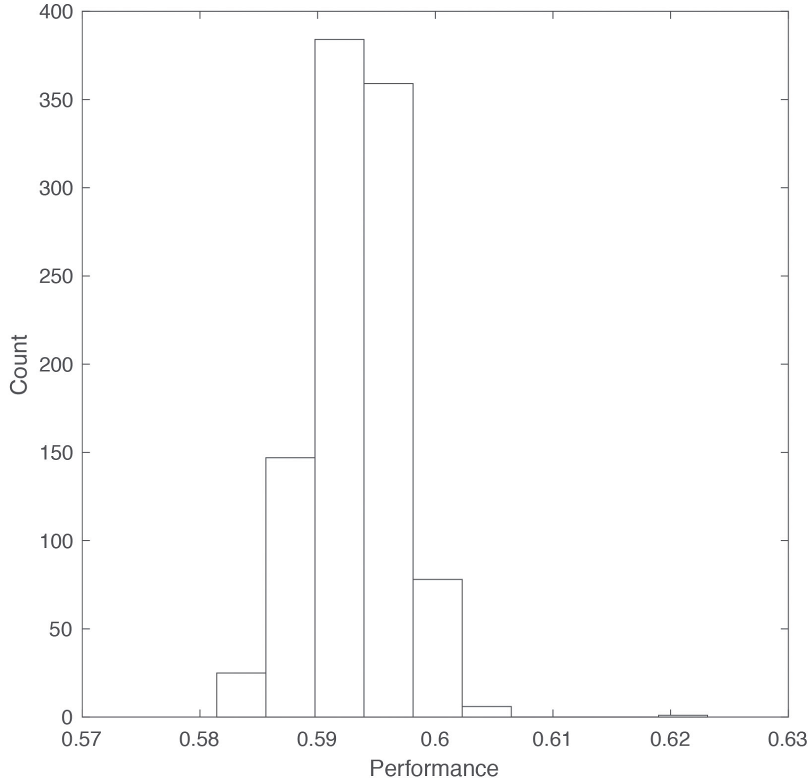

FIGURE 4 | Histogram of DDM performance accuracy. For 1,000 repeated selections of subsets of the data we used DDM to estimate the time a user would take to make a consistent decision (rejecting a user who was previously ranked 0–2 or accepting one who was ranked 8–10).

specific in their acceptance and men being more specific in their rejection.

Later on, the couple presumably focuses on the similarities and highlights the more nuanced features that would ultimately yield emphasis of religion, school, sports teams, and so on. This may be done either through the conversation, or as the users spend more time investigating the profile of the people they matched with.

DISCUSSION

In this work, we assessed the likelihood of two individuals communicating and potentially dating each other using mobile online applications. We estimated the potential of a pair matching based on various attributes such as education, religion, or psychological traits.

Our results show that individuals tend to gravitate, online, toward partners who share similar traits to them.

This tendency to select an effective match with partners who share traits, is shown in the realm of education, relationship preference, religious preferences, height, and essentially all attributes we investigated. Prior research has shown that people choose friends who are similar to them in a wide array of characteristics: age, race, religion, education level, socio-economic status, political leaning, aesthetic rating, or even handgrip strength (Dunbar, 2018). This is true for hunter-gatherer groups as well as modern societies. Our data therefore support the prior works.

In the context of mobile online dating, this similarity in traits is particularly interesting given that it is true even if those traits are covert on the mobile app (some of the parameters by which the pair end up being similar are not available to them at the time of the choice). This suggests that users end up figuring out who would be similar to them either by using silent and hidden visual cues or through the conversation following the initial choice.

Some parameters that users match on are likely to be the outcome of the geography or lifestyle settings. For example, iPhone users tend to have higher than average income than Android users. Therefore, the fact that we see an increase in EMR across iPhone users could simply reflect that users from similar socio-economic levels gravitate toward one another. More complex examples could be the indication of whether an individual is, for example, an introvert. This information is not overtly exposed to anyone at a brief glance of an image, yet influences the matching likelihood and, accordingly, must be communicated in alternative ways. Recent works in computer vision and psychology suggest that some personality attributes can in fact be gathered merely from the visual imagery (Cerf et al., 2008; Wang and Kosinski, 2018).

The understanding that similarity is predictive of effective matching is useful as it allows for an improvement

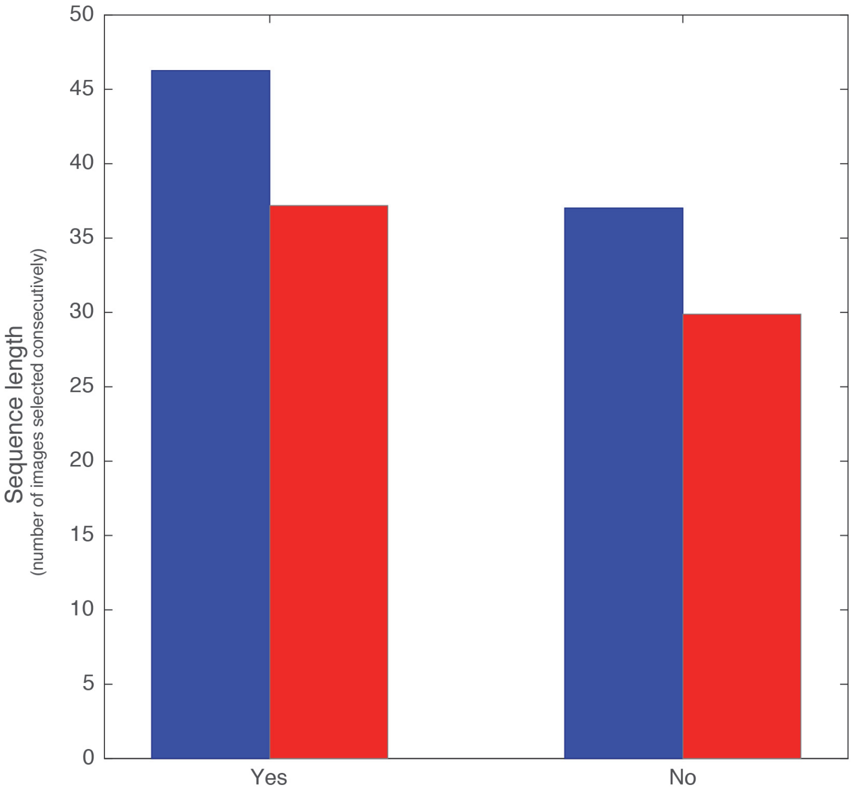

FIGURE 5 | Length of continuous sequence of accepting **(left bars)** or rejecting **(right bars)** a person by women (blue) and men (red). All *t*-test between all conditions show significance below 10^{-13}.

of the matching process and the scaling of the success rate of dating. The application of this can be either in the implementation and optimization of the matching algorithms to offer users more similar candidates to choose from, or it can allow users to make their selection in a more efficient way, as they would know their likely preferred match.

Given that (1) online dating is currently a major setting by which individuals meet, and (2) studies on couples who meet online suggest that online dating yields higher rates of satisfaction from the relationships and lower rates of breakups than traditional matching (Cacioppo et al., 2013), any improvement in the ability to identify a preferred partner is likely to lead to an increase in satisfaction. Borrowing from the literature on decision making and psychology, we can assume that if fit between products and personality increases happiness (Matz et al., 2016), then a fit between two individuals stands to yield an even greater increase in overall satisfaction. This is assuming that a choice of a partner is more personal and long-lasting, and that human connection trumps connection to non-human entities (companies, objects, etc.; see Mentovich et al., 2016). Indeed, prior works looking at similarity between people have shown that such alignment between individuals sharing psychological traits could, in fact, reflect an underlying neural synchrony that is likely to yield matching behaviors across various domains such as purchases (Barnett and Cerf, 2017) or political opinions (Barnett and Cerf, 2018).

Comparing Our Results to Existing Data on Matching

We compared our results to those of two domains that investigated the choice of a partner: assortative mating and traditional dating (i.e., meeting offline, speed dating, web-based online dating, etc.).

Assortative mating suggests that, in biology, partner selection is guided by tendencies to identify individuals with similar attributes (Jiang et al., 2013). While assortative mating typically focuses on genetic selection, the mating literature has shown prior evidence that seeking similarity or homophily in partners is often reflected in the phenotype level as well. Assortative mating holds across almost every characteristic that can be assessed in our data.

Looking at the early selection process alongside the ultimate match outcome, we see that users are not only similar to each other in their features, but also employ similar decision making strategies. Accordingly, we are able to use data on preferences by individuals to model the choice of a test group and predict some of the choice parameters.

Comparing our results to the literature on traditional dating, we are able to provide a unique reflection on the existing works. A notable advantage of our work is the size of the dataset investigated. Access to a dataset of this scale by academics is rare and nearly impossible without collaboration with industry. We used this opportunity to compare our results to existing data on web-based online dating, speed dating, in person dating, survey data, and matchmaking. Given that, as we noted earlier, in the last couple of years it is presumed that most dates in the Western world involve an online component—primarily online apps—it is useful to see how our results compare to earlier works. **Table 9** summarizes the literature compared.

Hitsch et al. (2010) also measured the effective match rate and estimated the parameters that led to a likely match. In their work the data came from online dating that is not on mobile apps. The data for an individual was richer since users were asked to generate a profile where they filled in additional details, such as body type (lean, muscular, over-weight, etc.), marital status (single, divorced, widowed, etc.), and numerous additional biographic information. However, the number of users and interactions is significantly smaller compared to ours. When comparing only the attributes that our datasets share, we note that the results seem to match. Hitsch's work has also shown that both men and women want to meet a partner with similar attributes. For example, users prefer similar education levels (the results were estimated using a maximum likelihood of the fixed effects using binary logit model, with the assumption that the first-contact and rejection costs are zero). However, Hitsch's comparison was between years of schooling rather than type of education. In Hitsch's data, women have an overall strong preference for an educated partner but also have a relatively small tendency to avoid men who are more educated than them. Men generally shy away from educated women altogether. Comparing our data to that of 10,526 participants in a dating service known as HurryDate (Kurzban and Weeden, 2005), which involves actual meetings alongside survey data, we see that participants have a preference for partners from the same age and religion categories. The focus in the HurryDate study was on age, body-mass indices, race, and marital status—all of which we do not use in our dataset. On height, which both our datasets compare, we see that both ours and Kuzban's work show a preference for men to be taller than women. Altogether, Kurban's work, which also shows a preference for couples who are similar in attributes to match, aligned with our results.

The works of Fisman et al. (2006, 2008) looked at another coupling method—speed dating—and showed that individuals tend to prefer others who come from regions comparable in population size. The other parameters measured involved income, race, SAT scores, and other sets of information which we did not have access to. This, too, aligns with our data, although our results are biased by the matching algorithm's tendency to suggest local/nearby candidates, thereby altering the likelihood of choosing a partner from other locales with different population sizes.

Our work also aligns with existing literature on arranged marriages. Looking at the overall likelihood of marriages to last (measured by years until divorce), arranged marriages of couples who share religion, education, or who have height differences similar to the ones noted in our results, have a higher likelihood of lasting longer. These couples are also the preferred option by matchmakers (Etcoff, 2011). Note that arranged marriages are mostly popular outside of the United States, making the comparison to Hinge skewed (since virtually all the data we examined come from the United States).

Other prominent works in the field of match assessment focused on race (Fisman et al., 2008), income (Buss, 1989; Fales et al., 2016), weight, and prior declared preferences by the individuals (see Eastwick and Finkel, 2008 for a comprehensive discussion), all of which we had no access to in our dataset.

Note that race, specifically, was shown to be a significant driver of coupling in prior works, with the majority of pairs selecting a partner from the same race [however, the increased use of online dating has been shown to correlate with greater numbers of inter-racial couples (Ortega and Hergovich, 2017), presumably due to increase in encounters between people who would otherwise never met, creating connections with unassociated social groups and reducing the isolation of groups]. Prior work on dating apps has shown that White/Caucasian men and Asian women are the most popular selections (Bruch and Newman, 2018), while Black/African Descent women and Asian men receive fewer matches.

We did not analyze race similarity (appears in our dataset as "Ethnicity") aside from examining the frequency of initials within a certain ethnicity. However, given that the strongest driver of coupling in our data was religion, which often correlates with ethnicity, we suspect that the similarity in ethnicity/race is likely to be true in our data as well.

When examining works on the ISM (Fletcher et al., 1999; Campbell et al., 2001) the user attributes we examined can be viewed as representing the ISM characteristics (warmth-trustworthiness, vitality-attractiveness, and status-resources) in a variety of ways. It would stand to reason that those who have the same education, for example, may also share status (especially in higher degrees). Similarly, two people of the same religion could be seen as aligned on their trustworthiness virtue. Similar height could be a marker of attractiveness, etc. Therefore, the selection of an individual could be seen as a selection aligned with ISM attributes.

Given the high agreement between all the datasets on the outcomes, Finkel (2017) suggests that if a person is interested in optimizing their chances of identifying an effective match, mobile online dating should be the preferred option. That is, given that the results from all works are similar, but the scale of online dating is bigger, using dating apps would yield the highest return on the time and effort invested. Importantly, research looking at the algorithms used by online dating platforms to offer improved matching outcomes has shown that these algorithms prove unsuccessful in predicting a likely effective match based on stated preferences (Finkel et al., 2012; Joel et al., 2017). However, given our results we can suggest that potentially including in those algorithms a weight-function that increases the likelihood of successful coupling by individuals who share certain attributes instead of focusing on stated preferences may prove beneficial in yielding a greater number of effective matches.

TABLE 9 | Literature.

Medium investigated	Features investigated[1]	Sample size	Share	Key finding	Publication
Traditional in-person encounters	Preferences, Age, Income (Resources), Attractiveness	10,047 (33 countries)	30–60%	Mechanisms underlying mate preferences are similar across individuals. (But manifested in different attributes. Females value resources whereas males value reproductive capacity)	Buss, 1989
	Age, Income, Education, Attractiveness	27,605		People prefer individuals who are similar to them.	Fales et al., 2016
Match making/arranged marriages	Attractiveness (but also Preferences, Height, Religion, Education)	N/A (review)	<1%[2]	Similarity leads to longer and happier marriage.	Etcoff, 2011
Speed dating	Preferences, Income, Attractiveness	163	1%	No differences in the associations between participants' romantic interest in real-life potential partners (met during and outside of speed dating) and the attractiveness and earning prospects of those partners.	Eastwick and Finkel, 2008
	Education, Income, Race, Original location, SAT-scores	348		People prefer individuals who are similar to them. (But females value intelligence, race and locations indicative of higher income, whereas males value attractiveness).	Fisman et al., 2006
	Race	412		People prefer individuals who are similar to them.	Fisman et al., 2008
	Preferences, Age, Race, Height, Body-Mass indices, Religion, Sexual preferences	10,526		People prefer individuals who are similar to them. (Both females and males value primarily observable features rather than harder-to-observe such as education, religion)	Kurzban and Weeden, 2005
Web-based online dating Match.com, OkCupid, JDate, etc.	Preferences, Education, Age, Income, Race, Ethnicity, Religion, Original location, Employment status	19,131	17–20%	Couples who share traits have higher rates of satisfaction and lower rates of breakups.	Cacioppo et al., 2013
	Rich data on individuals (profile with numerous fields)	5,787		People prefer individuals who are similar to them. Features aligned with our work: education, marital status	Hitsch et al., 2010
	Education, Age, Income, Race, Religion, Network ties	U.S. Census		People prefer others who share similar traits. (also, those traits lead to more likely marriage and higher satisfaction; However, people prefer inter-racial selection if the network is small) Features aligned with our work: education, marital status	Ortega and Hergovich, 2017
Online mobile dating Hinge, Tinder, Bumble, etc.	Attractiveness	186,935	40–70%	People prefer others who align with them on attractiveness.	Bruch and Newman, 2018
	Preferences, Personality traits, Education, Height, Religion, Height	400,000,000		People prefer individuals who share similar traits.	Our work
Biology	Preferences, Immune system, Strength, Genetics	N/A (Review)	N/A	High likelihood of pairing for *compatible* features, primarily immune systems, genetics and evolutionary indicators	Andersson and Simmons, 2006
	Genetics	58		Attraction is driven by genotype alignment, odor preferences and histocompatibility	Santos et al., 2005
		254 species		Animals show 28% correlation in phyla.	Jiang et al., 2013

(Continued)

TABLE 9 | Continued

Medium investigated	Features investigated^1	Sample size	Share	Key finding	Publication
Relationships	Personality traits (extroversion, neuroticism, etc.)	1,101		People prefer individuals who are similar to them.	Youyou et al., 2017
	Preferences	N/A (Reviews)		People preference novelty in the early stages of relationships.	Finkel, 2017
Marriages	Preferences, Education, Age, Income, Race, Religion, Attitudes, Intelligence			People prefer individuals who are similar to them.	McPherson et al., 2001
				People prefer individuals who are similar to them. (and inequality leads to likely dissolution)	Schwartz, 2013
	Preferences			People seek complementary (/opposite) characteristics	Winch and Goodman, 1968

Alignment of our work with existing literature looking at similarity between partners in mate and dating selections on various features. The list samples works that show similar method or dataset to ours. [1] List includes: Preferences, Personality traits, Education, Age, Income, Race, Ethnicity, attitudes, Intelligence, Attractiveness, Height, Body-Mass indices, Religion, Original location, SAT-scores, Network ties, Sexual preferences, Immune system, Strength, Genetics. [2] In the Western world, but higher numbers in religious and traditional communities, (primarily outside of the U.S.). If we include a friend 'introduction' it climbs to 5–15%.

Matching Attributes

The initial likelihood of a conversation occurring between two users in our dataset is 1 in 200 (0.51%). This is already substantially higher than the number of conversations a user is likely to spark on an average day (i.e., commuting in a metropolitan area, dining at a restaurant, or having a drink at a bar). To study the nuances of EMR beyond this baseline, we estimated the various features in our set and their independent contribution.

First, we assessed the likelihood of a couple choosing each other based on their preference toward liberal arts colleges. Users who are both from liberal arts colleges matched effectively almost 40% more than pairs where only one was from such a college. We reason that users who went to similar schools likely participated in similar activities or had similar interests, which could be reflected in their photos and biographical information on the app. Therefore, in future communication on the app they would likely have a shared starting point for connection and conversation and have a sense of familiarity which, in turn, could become a driver for future communication (Shalizi and Thomas, 2011). Less clear is why liberal arts students would match more with attendees of unranked schools than with non-liberal arts colleges. One theory could suggest that students of more competitive institutes of higher education would match more effectively with each other than with those that do not make the ranking. Another possible explanation is that men prefer women who are less educated than they are as suggested by Hitsch et al. (2010).

Looking further at education, we see that Ivy League students show similar effective match patterns to liberal arts college students. Matching among Ivy League students is nearly 65% higher when one of the users is not from these eight schools. Given that the eight Ivy League schools have, historically, been pitted and compared with each other for decades it would seem likely that people who have earned the prestige of attending them may look for similar partners.

The likelihood of NCAA conference participants effectively matching (ranging from 7% increase above average EMR for those students from "Big Ten Conference" schools to as much as 91% increase for students from the "West Coast Conference") is high as well. This could be explained partially by the fact that schools that participate in the same NCAA conference are generally in the same geographic area, or that the topic of sports tends to act as an introductory topic of conversation. Generally, sports teams and players have long had a culture of devotees that connect and engage around them—from European football clubs to American sports bars. People select their social circles, weekend activities, or the colors of their outfits based on their affiliation to sports teams. This may also drive users to end up sharing similar preferences in our dataset.

Mobile devices and their relationship to effective matching have potentially interesting implications. User similarity in mobile preference yields a higher likelihood of an effective match; however, the effect is small (0.01% increase. Cohen's D: 0.21). While our dataset has almost 300 million potential matches between iPhone users, the mean effective match rate was 0.12%, which is lower than that of Android users (0.13%). These numbers are higher than the EMR of users with different devices (0.11%). While some research suggests that a person's mobile device reflects potential trends, character traits, photo-taking preferences, and writing style (Grant, 2017), an alternative hypothesis to the reason behind such match proportions could be merely geographical or socio-economic. Indeed, data from Twitter usage, which contains the device used for the post, suggest that iPhone users often cluster on the coasts and within major cities in the United States, whereas Android users are elsewhere (Edwards, 2014). A likely combination of all theories — usage of mobile device pertaining to a certain income, geography, and style — could be the driver of these matches. In itself, this result is curious given that it is assumed that the choice of device usage during the matching process is not relevant to a partner's choice, nor is it revealed explicitly during the conversation.

Testing the phenomenon of implicit egotism on the national level by exploring the effects of users' initials on effective matching is consistent with results from prior work (Jones et al., 2004) in showing that individuals with shared initials tend to gravitate toward each other. Our results show that effective matching among those individuals is 11.31% higher than among individuals who do not share the same initials. Compared to population results showing that marriage percentage across such individuals is 8.81% above chance, our results trend in the same direction.

It is important to note that skeptics of this phenomena have expressed concern that implicit egotism may be driven by name frequency in specific regions and ethnic groups since users who share a specific faith or ethnicity are more likely to share a common last name. Given that we *did* have ethnicity data for users, we investigated the effect of ethnicity in this context. In our data, users identifying as Jewish are 670% more likely to have a last name beginning with "S" and 223% more likely to have a first name beginning with "J" than a user identifying as Muslim. Similarly, users identifying as East Asian are 152% more likely to have a last name beginning with "L" than users self-identifying as White/Caucasian. Under such conditions the effect of implicit egotism may be a byproduct of a preference for religious and/or ethnic identification. As we did not have full access to ethnicity/race data in our analyses, we normalized our results by religious affiliation proportions as a proxy for ethnicity. The effect remains the same.

When examining religious orientation as it relates to effective matching, it is not surprising that people matched more often with users that had a shared religious affiliation (EMR = 0.21%) than with users whose religions differed. Religions that had smaller representation on the app had the highest rate of effective matching. Muslims, with only 3,741 potential matches (0.0009% of all possible matches) had an EMR of 0.94%. Hindus (0.08% of all possible matches) had an EMR of 0.61%. Both are significant ($p < 0.01$) in comparison to the average EMR of 0.12%. Every other group had over 500,000 potential matches but a lower EMR. Interestingly, the data show that, across religions, men were more selective (2.97%) than women in dating outside the religion. The only exception is Judaism. This may be accounted for by the fact that in Judaism the religion passes from the mother, not the father (Mishnah, Kiddushin, 200AD). As such, it may reflect a greater pressure on Jewish women to date men who share their religion.

When looking at the stated preferences in relationship type, it greatly reinforces the value proposition of mobile dating apps when people who have aligned desires actually have higher effective matching rates (EMR = 0.15–0.20% depending on desired relationship type). If a user desires a committed relationship it would reason that they are more likely to engage in conversations with those who have aligned preferences. Additionally, it may be the case that those who are interested in, for example, casual relationships would have different conversation styles and different sets of needs from the conversation. These disparate styles may be intuited from the conversation and drive the ultimate EMR.

Investigating the relationship between introversion/extroversion and matching shows that introverts rarely connect with other introverts. While the users initially show matching preferences for each other based on profile features, neither is likely to start a conversation. If one of the users is an extrovert, we see a significant increase in effective matching (71.9–157.5% increase in EMR). This effect correlates with the level of extroversion the two users exhibit (higher score in extroversion above the mean correlates with increase in EMR; $r = 0.52$, $p = 0.03$). Two extroverts are more likely to engage in a conversation leading to an effective match than if only one of them is extroverted. While social traits were studied extensively in the context of engagement in group relationships (Cain, 2013), their effects on dating preferences were not investigated thus far to the best of our knowledge. This work suggests a potential connection between personality and dating preferences that is different from those offered in the personality literature. This may imply that although introverts are able to "step out of character" in some social settings, the difficulty with dating is that they are interacting with strangers and have no basis of familiarity.

One should consider that this social ratio could actually function as a proxy for other measures of a user's characteristics. For example, these may reflect how attractive a person is. Given that existing research shows that more beautiful people are more likely to find mates (Langlois et al., 2000), we explored this option as well. Our data do not support the theory that attractiveness is the driver for friend count. That is, if this alternate theory was correct, we would expect that people generally match with others with the same social ratios. This is not the case. Men with very high social ratios match with women who have very low ratios in high proportions and vice versa (**Figure 1**). Although social ratio is not a perfect proxy for introversion and extroversion, it provides a reasonable estimate and valuable insight into a link between personality traits, and effective matching.

Previous research on height as it relates to dating suggested that men and women prefer mates who have a specific relative height to their own (Pawlowski, 2003). Aligned with prior works, our data show a complex relationship between men's and women's heights (**Figure 2**). Women seem to prefer men taller than them but, given that height follows a normal distribution, there is not an unlimited supply of extremely tall men. As a result, we see a scarcity effect manifested in the data: women of a certain height may match most effectively with men of a specific height, but those same men may match effectively with women of a different height. Given that information in the matching experience is not fully available (i.e., a tall woman, for example, is not aware of the number of taller men and the likelihood of their emergence) the model for a user's preference on height is skewed by the available resources. This drives the equation for matches among people of similar heights to be non-linear. Therefore, while we do not rule out the large contribution of height to desirability — especially for men — this does not guarantee an overall increase in EMR as suggested before.

Early Decision Making Process

Beyond examining the EMR which reflects the outcome of a choice, conversation, and complex decision making heuristics, we looked at the attributes of the early decision process. These attributes reveal the considerations that go *into* the choice set and, presumably, affect the ultimate EMR. We focused on looking at whether men and women exhibit similar choice strategies with respect to consistency, response time, and streaks.

When comparing selection time (the time necessary to evaluate a potential partner), men's and women's strategies demonstrated significant variation in making an affirmative selection but were consistent when declining individuals. Women took a significantly longer time to accept a person that others typically rejected. That is, the tradeoff between speed and consistency is notably hindered with women on the side of accepting a low-ranking man, and notably improved when rejecting one. Men's selection time is consistent for acceptance/rejection.

Given that Hinge caps the number of choices per day, making a streak of, for example, 45 "yes" choices to occur over multiple days, we could not estimate the choice memory/bias in full. While we think that a user's 16th choice is influenced by their 15th choice, there is a chance that they are days apart in reality. With that in mind, we looked at streaks to see if they are similar among men/women. Women's average longest "yes" streak is 46.3 choices long. Fewer women are likely to go on such a streak of saying "yes" (1.3%). The majority of women (43.1%) are likely to have their longest streak of saying "no." The average longest "no" streak has 37.02 choices. Men are equally divided between those whose longest streak is of saying "yes" and those whose longest streak is saying "no" (26% "yes" and 24% "no"). Altogether they tend to alter their opinion more frequently and say "no" on average, to less than 30 women consecutively (**Figure 4**).

Importantly, we assume that the potential partner to choose from appears at random. However, given that the options come from a pool of candidates that are tailored by a matching algorithm, we cannot rule out the possibility that a "yes" streak is the outcome of a successful algorithm that rendered a sequence of ideal choices. Our intuition is that a long streak is likely a reflection of a user's behavior. This is especially true when comparing genders, as the same matching algorithm is at play.

It is noteworthy that Hinge's limit on the number of selections a user can exercise within a day is likely to strengthen the robustness of our results. That is, while the decision making strategy a user exercises in a finite domain could be different than the one made in an infinite choice horizon, we expect that having a limited number of attempts at a successful effective match would yield a more thorough vetting process. This is supported by recent data pertaining to the selection strategy employed in online web-based dating (Tyson et al., 2016; Bruch and Newman, 2018).

Additionally, while the limitation on the number of candidates a user sees each day may change the strategy they employ for the choice, it is unlikely to affect the chances of actually meeting the pool of users in a certain geolocation. That is because (1) Hinge extends the pool of candidates offered beyond merely the Facebook "friends of friends" when the pool of options is exhausted, and (2) including a user's 2nd and 3rd degree connections within a certain geolocation is likely to incorporate the majority of users in that location. Put differently, if for example, a user lives in Toronto and is faced with a choice of another user on a dating app such as Tinder or Bumble, it is likely that the person they are viewing is also in their "friends of friends" circle on Facebook and therefore a potential match on Hinge as well. That is simply because of the estimates on the number of degrees of separation between any two individuals on Facebook. Facebook research shows that any two Facebook profiles are, on average, 3.5 degrees apart, and that this number likely decreases to 2–2.5 if the friendship circle is confined to a geolocation (Edunov et al., 2016).

Although our results reveal differences between the genders in selection style, these differences are minor when examining their overall outcomes. A striking result that emerges from our analyses is how consistent people are and how less unique their choices are compared to perception when it comes to partner selection. The fact that a simplified model based essentially on prior selections by users can predict both the choices and the response times of multiple individuals with accuracy of nearly 60% suggests that people are more predictable in their preliminary choices (accepting individuals that peers liked and rejecting ones that they did not) than often stated. Therefore, the idiosyncrasies and the convergence to similarities presumably happen later in the communication.

Limitations

Our work has a few limitations. First, given that our dataset relies heavily on Facebook as the platform populating the user profile, it is important to note that existing works looking at the alignment between a user's online and actual character are not perfect. While it is unlikely that a person would be entirely different on their online profile (as they are likely to be called out by their friends for such discrepancy) studies show that users do tend to exaggerate various attributes of themselves on their public image. Our study is, therefore, bound by the variance between the actual user profile and the depicted one. These differences are likely to be particularly pronounced in the context of extroversion (Amichai Hamburger et al., 2002; Mitchell et al., 2011).

Second, some attributes in our dataset have notably fewer samples than others and therefore should be interpreted accordingly. However, with the exception of NCAA and religion (within which only Muslims had low count) all our metrics included at least 100,000 potential matches and typically included over 1,000,000 samples if not one order of magnitude more.

A third limitation could be attributed to the way we define an effective match. We concluded that a match is effective when the two people in the conversations exchanged contact information. However, there could be alternative ways of setting a meeting that do not involve these. In order to maintain our decision to not read user messages and merely use regular expressions to infer if contact information was exchanged, we decided to refrain from including those alternative modes of setting an offline encounter (i.e., using the mobile app exclusively for all communication). Our results, therefore, act as a lower boundary to the proportions of effective matches that happened in our dataset and could be adjusted if future work could observe the conversation's content.

Fourth, a large number of user profiles did not include all possible fields. Therefore, our results may be skewed toward individuals who were willing to disclose certain details. Additionally, the results are reflective of a complex selection process where missing information may or may not play a significant part. We do not know whether the inclusion of more information on a specific user would have increased/decreased the chances of them effectively matching and are limited to estimates within a specific attribute rather than across attributes.

Finally, despite the alignment of our results with various other types of dating sources (i.e., speed dating, actual meeting, survey data, match-making, and arranged marriages), it is noteworthy that our analyses are based solely on data collected from the Hinge mobile app, and caution should be exercised when generalizing the results to other mobile dating apps and populations. Some notable differences between Hinge and other prominent dating platforms pertain to the user demographics and choice architecture. For example, Hinge's demographics is primarily heterosexual and therefore may not generalize to homosexual communities. Similarly, Hinge's matching protocol does not impose rules on which gender is required to initiate a conversation or impose a time limit to a communication. Those differences may alter the choice dynamics. Some may strengthen our results (i.e., Hinge's limit on the number of choices per day may make each choice more deliberate) and some may weaken our results (i.e., the requirement for additional fields in the profile may drive some users away from using the platform). We illustrate the key differences between Hinge and other leading mobile dating apps in **Table 10**.

Future Work

Additional work might focus on features that are not labeled in the data but could potentially be inferred (either from the imagery, natural language processing, or social network data) and enhance our understanding of a user's early priorities. Visual cues that could be analyzed may involve the style of the images available on the dating app, whether a person smiles or not, and aesthetic matches between pairs.

Natural Language Processing (NLP) cues could refer to the style of language used in the communication, such as length, usage of graphical icons, typos, grammar, etc. Primarily, since our results show broader choice strategies across men/women in the early stage followed by a narrowing of choices to arrive at a specific EMR, we can suspect that numerous additional pieces of information are brought up during the conversation that navigate the convergence. It would be interesting to investigate the conversations with the goal of unpacking the cues that users send to each other to signal their preferences. This is especially interesting if the information is not overtly discussed (i.e., if no user specifically asks the other "what religion do you subscribe to?" but then ends up matching with people who share their religious beliefs). More complex learning that can potentially be inferred (i.e., whether the two individuals smoke, share an interest in similar music, vote similarly, or share earning capacity) by analyzing the profile information may be used to enhance our understanding of whether similar traits lead to higher effective matching.

More complex NLP analyses might be used to reveal differences between the stated preferences and true intentions for a partner (i.e., an individual says that they are interested in dating for the purpose of a long-term relationship but seem to behave as if they are interested in a casual encounter). Accordingly, we can see if the similarity in actual preferences yields higher matches than the similarity in stated preferences.

Furthermore, our analyses assumed that the exchange of information on the mobile dating app is likely to be an indication of an interest in a romantic relationship and the exchange of information was an explicit way to arrange a date. This is not certain. Therefore, a future direction could look at what proportion of a conversation that culminated in the exchange of communication information indeed reflected a desire to meet in person for a romantic purpose.

Social network data could be used to learn whether group influence (shared friends, shared experiences, status within a group, etc.) are predictors of a successful match between two individuals. This could even be used to learn whether a person's friends are valuable predictors of a successful match when the individual does not select his/her partner themselves, as suggested in prior works (Gilbert et al., 2009).

Given that our results were compared primarily to other matching protocols such as speed dating, matchmaking or arranged marriages [but also to the recent work by Bruch and Newman (2018) which highly aligns with our demographics as it focused on online dating in urban cities within similar population and age groups], it is worthwhile to continue observing the trends and data from additional popular apps, especially ones that focus on demographics outside of the ones observed in our work (i.e., homosexual communities, rural communities, or communities outside of Western societies).

Connection to Neural Models of Choice

Drift diffusion models are frequently used as a proxy for the way decision making is conducted by neural mechanisms in our brain. An illustration of such a decision making model depicts the aggregation of information about the choice from the moment a user's eyes land on a user profile to the moment their fingers swipe the phone to reflect their choice. Detailing the steps involved: a user's visual cortex receives incoming input from the eyes about the option they are faced with on the phone's screen and processes the information in order to decide whether to swipe left or right. Neural sites in the brain aggregate the information from the eyes alongside other cognitive internal processes and utilize a directed random walk to navigate the relative decision value assessment (Krajbich et al., 2014). Accumulated information is internally evaluated and drives the process, according to the weights and values of certain attributes and, ultimately, approaches a threshold for a decision. Once the threshold is crossed the conscious choice is manifested.

An interesting venue to follow would be to apply the DDM in the context of neuroscience in similar ways to which other binary choices were previously tested in humans and apes (Gold and Shadlen, 2007) to see if mating preferences follow similar choice processes. This would allow us to track the decision

TABLE 10 | Popular mobile data apps.

Characteristic	Hinge	Tinder	Grindr	Bumble
Estimated percent of US online dating market engaged with app at the time of the study	1.1%	25.6%	6.3%	3.6%
Popular location	Primarily Urban	Most U.S. locations	Primarily urban (but available everywhere based on geolocation)	Primarily urban (but available everywhere based on geolocation)
Protocol	Parties mutual swipe exposes the chat option	Parties mutual swipe exposes the chat option	Users do not swipe but are presented with a grid of potentials 3 wide and length is dependent on subscription level. They can chat with these users immediately	Parties mutual swipe exposes the chat option only women can initiate the conversation
Primary user group	Heterosexual	Heterosexual	Homosexual Men	Heterosexual
All users	Heterosexual, gay, lesbian	Heterosexual, gay, lesbian	Homosexual Men, Women (~6%)	Heterosexual, gay, lesbian
Positioning	Dating	Dating	Sexual partners and Dating	Dating
Choice limitation	10–21 selections per day (exact number determined by an algorithm)	100 selections confirming interest per day for the free version	100 people to chat with for the free version	50–100 swipes, number could fluctuate based on user patterns of behavior
Additional limitation	If communication does not occur after a fixed period of time the match will expire	None	None	Imposed time limit on response Women have 24 h to initiate the conversation or the match expires. After women initiate, their matches have 24 h to respond or the match expires
User data source	Populated by Facebook. Users can fill out additional dedicate fields such as height, relationship preference, religious affiliation, etc.	Options: (1) populated by Facebook, (2) associated to phone number/email address and populated manually	Options: (1) populated by Facebook (2) associated to phone number/email address and populated manually	Options: (1) populated by Facebook (2) associated to phone number/email address and populated manually
User data fields (all of these attributes correspond to the data at the time of the study; The user interface may change)	Users can fill out additional dedicate fields such as height, relationship preference, religious affiliation, etc.	Users have an About me section they can fill with any information (not verified)	In addition to a basic about me, users can provide Height, weight, Tribe (this is what type a person is within the homosexual community), Body type, Ethnicity, Looking for, and Relationship status	Users have an About me section they can fill with any information. Now: There are additional fields for Height, smoking, desire for children, etc.

making pathway with increased precision. For example, given prior estimates on the time it takes a visual cortex to process the input from the retina (approximately 120 ms; Mackay et al., 2012; see **Figure 6**), the additional time it takes the Fusiform Face Area (FFA) to process the face imagery (additional 40 ms), the time it takes the supplementary motor areas to plan, initiate, and execute the movement of the finger (additional 120 ms), and the estimate of additional processes, such as perception, reading, eye movement (in the case of scrolling), etc., we can narrow the time an individual user spent on the choices. In the example we illustrated here, subtracting the likely 500 ms for the perception/movement from a woman's selection of a highly qualified (ranked above 8) man (average of 3.19 s; **Figure 3**), we can look at the rapid choice and suggest that the time allocated to the actual choice was close to 2.69 s, on average. This allows us to estimate the mental processing given to each decision and to incorporate that into our model.

Accordingly, an extension of this work could go beyond the realms of dating and onto studies of preferences. One could look at online mobile apps that match users for purposes of work, collaboration, or other social interactions. We might learn that a choice of, for example, hiring an employee, takes equal time whether elaborate thinking goes into it or whether it is done in fractions of a second. This might suggest that the notion of homophily and tendency for presence of similar characteristics are at the heart of more of our decisions.

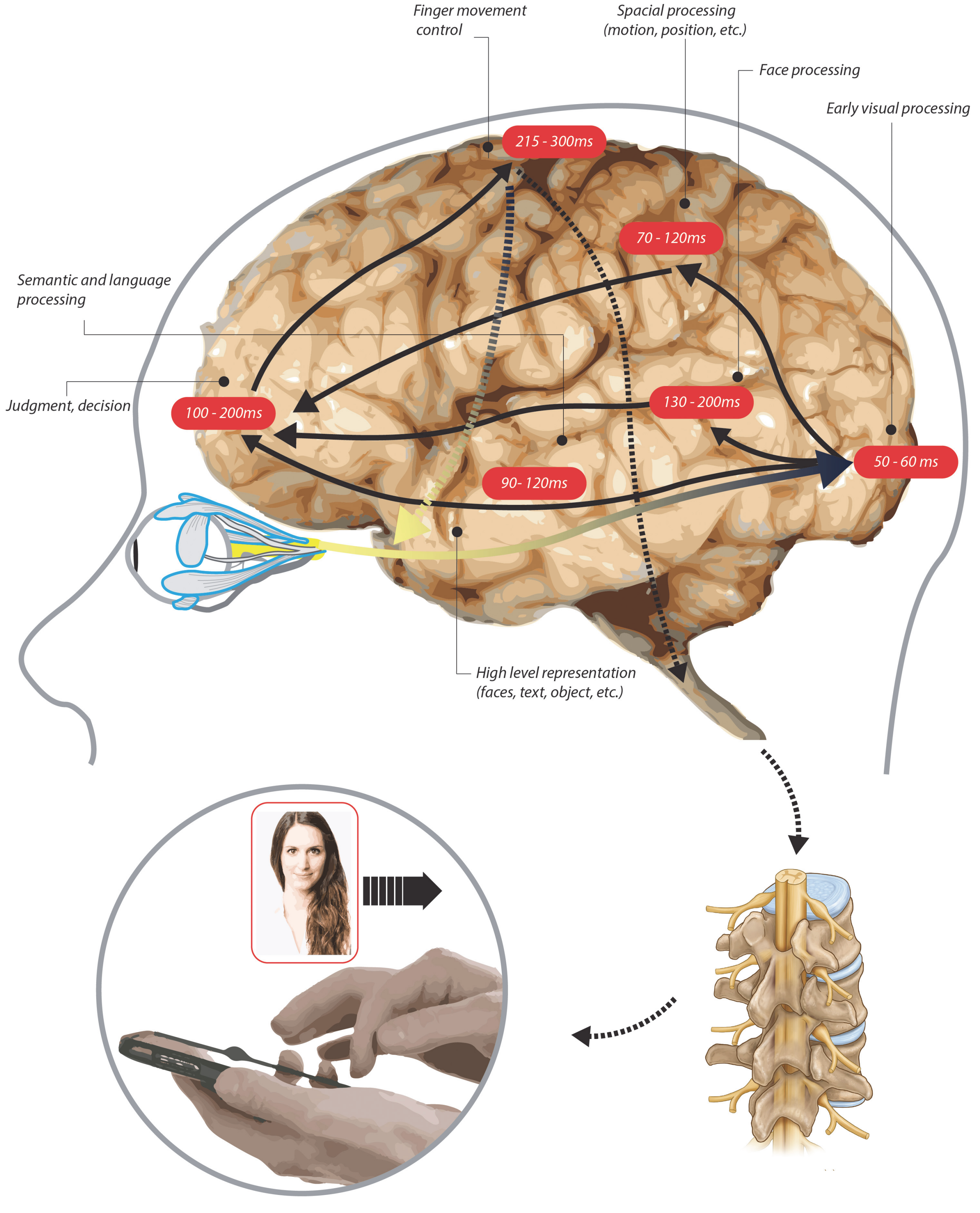

FIGURE 6 | Continued

FIGURE 6 | Illustration of the decision process and its latencies. Neuroscience estimates on the latency of information processing in the brain suggest that information from the retina is processed at the visual cortex within about 50 ms from the moment a person views an image (e.g., a picture of a person on the Hinge dating app). The information is then assessed in the "where" and "what" pathways within 50 ms more and, given that the images include the face of a person, is processed at the Fusiform Face Area within about 130 ms. Information from all pathways is ultimately aggregated at the prefrontal cortex where a judgment is potentially made. The choice is manifested as a motor control signal at the supplementary motor area which is communicated via the spinal cord to the fingers that swipe left/right to execute the selection. This process should typically last at least a third of a second. However, alternatives to the immediate choice could involve feedback from the Frontal Eye Field to the Superior Colliculus that drives an additional saccade of the eye to a different location on the screen (which, in turn, initiates a repetition of the processing), scrolling the phone screen for more information (using the motor controls) or additional high-level semantic processing (i.e., reading the text on the screen). All of those actions add additional time to the processing. Our results — combining the estimates of the decision making times using the DDM with an investigation of the average decision time allocated to all choices on the app — suggest that the initial selection happens rapidly and is based mostly on salient information. Given that the ultimate EMR reveals a strong preference for partners sharing attributes, information about the homophily could be gathered subconsciously from cues in the app that are indicative of preferences, or through the chat that happens throughout the communication.

CONCLUSION

Discovery of potential romantic partners is currently dominated by mobile apps. These apps rely on similar methods for choosing a partner and offer a set of properties by which one can select and identify a potential match. While the information offered about an individual might differ across platforms, the majority of dating apps focus on a combination of visual imagery and a small number of features describing a user's background and intentions. Algorithms for improved matching and the promise to help a user find their ideal match make the online dating industry flourish and occupy hours of some users' days.

Combining our assessment of the early decision with the ultimate EMR, our results suggest that the saying "opposites attract" might not be true. On the contrary, individuals seem to gravitate toward partners that share traits with them. This is consistent with research that tested similarities between individuals in the context of choices, dating (Fiore and Donath, 2005; Skopek et al., 2010; Anderson et al., 2014), voting (Graham et al., 2009; Barnett and Cerf, 2018), and behavior (McPherson et al., 2001). Some works have linked the preference toward like-minded individuals or people who share key attributes with others to evolution, and to genetics. Some studies even suggest that identical twins who were separated at birth end up sharing some personality traits, behaviors, and preferences years later (Plomin et al., 1994; Jang et al., 1996; Rhee and Waldman, 2002). However, looking at datasets of the size we show here was challenging up until recently.

Thanks to the popularity of mobile apps that increase the amount of labeled data, and owing to the fact that the era of big data offers a set of readily available tools for loading and analyzing large datasets, we could investigate preferences in the context of dating on an unprecedented scale.

Our work contributes to the knowledge on mating choices in multiple ways. First, we show which parameters contribute to a likely match and their weights. Second, we show that a choice to move forward with interacting with a person or rejecting them can be estimated using a simple binary decision making model. Third, we show that, while the experience of online dating is quite different than that of other types of dating (i.e., in person meeting, or speed dating), the outcomes are similar. That is, in the course of seconds of exposure to a potential date, users are able to make a choice that parallels the one they would have made if they met the person in, for example, a bar. This suggests that online dating apps offer an advantage compared to offline methods of dating in scale. Because the pool of compatible partners increases dramatically, one can increase the return on invested time and effort and focus on a pool of individuals that match their preferences from a broader set of options. Although people may spend little time interacting with each profile on online mobile apps, they actually learn a significant amount about each other. Given that the world we live in is heading toward a more fast-paced nature of media and consumption (Cutting et al., 2010), these dating apps might dominate the dating sphere in the future.

This study is the first to explore the phenomenon of effective matching and dating preferences at such a large scale. After reviewing more than 421 million potential matches and examining this collection of proprietary data, we were able not only to replicate and validate the results of previous works, but also further push our understanding to realms not explored previously.

As we continue to see more of the population moving toward the use of mobile dating, developers and algorithm designers who are interested in maximizing the effectiveness of potential matches should accordingly design around similarities. However, taken to the extreme, this can lend itself to exclusion by various demographic characteristics and increased convergence to echo-chambers. We would encounter partners with higher alignment but be less exposed to opposing views and diverse personality characteristics. In light of this risk, it may be beneficial for society if apps were to present both similar options as well as intentional diversity.

As our knowledge on the topic grows and we continue to explore the data that drives our relationships, it would be unsurprising if the next generation of digital supported dating technologies moved toward Machine Learning and Artificial Intelligence tools that would eliminate the need for us to make selections ourselves. These would, instead, learn our priorities, weigh our decision processes, and emulate them.

It has not escaped our notice that in such a future we may be able to discover an ideal partner with the same simplicity as other current online experiences (i.e., ordering food or purchasing products online). People would open an app, provide access to a collection of personal data, and moments later their ideal mate would appear looking to schedule a first meeting.

Accordingly, some researchers identify a change in dating and commitment altogether, which may lead to an entire shift in the structure and social construct of pairing (Finkel, 2017). As a society, we could use results such as the ones provided here to either redefine the meaning and expectations from a match or adjust our understanding of the purposes of a relationship to a reality where alternatives are always nearby and stability in relationships is less frequent.

AUTHOR CONTRIBUTIONS

DM conducted all the analyses. JL and MC wrote the manuscript and conducted some of the meta-analyses.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2019.02010/full#supplementary-material

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Pair-Bonding as Inclusion of Other in the Self: A Literature Review

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This article surveys scholarship on the self-expansion model principle of inclusion of other in the self (IOS) as it relates to long-term pair-bonding (i.e., enduring adult romantic monogamous relationships). First, we introduce the concept of IOS and then provide a brief overview of prior research. We then review compelling extensions and findings related to relational concepts such as perspective taking (Bernstein et al., 2015), social comparison (Thai and Lockwood, 2015), self-determination (Weinstein et al., 2016), humor (Treger et al., 2013), and pain contagion (Martire et al., 2013). Next, we explore two recent theoretical directions of the principle—the two-dimensional model of relational self-change (McIntyre et al., 2015) and the perceived inclusion of the other in the self (IOS-perceived) construct (Tomlinson and Aron, 2013). Considering these findings and their relation to pair-bonding, we propose important future directions of the IOS principle of the self-expansion model.

Keywords: pair-bonding, self-expansion model, inclusion of other in the self, closeness, relationships

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Pair-bonding, in the context of enduring adult romantic relationships, is the observable behavioral manifestation of an intra- and inter-psychic process of connecting with one's partner. It is important to explore the psychological mechanisms that influence human adults to pair persistently and romantically with a specific other. One such mechanism is the self-expansion principle of inclusion of the other in the self (IOS). The self-expansion principle portends that close relationships provide opportunities to expand the self, as within relationships, each partner experiences the resources, perspectives, and identities of the other partner as to some extent one's own. The other is to some extent "included in the self" (Aron et al., 1991). Thus, the cognitive construction of the other merges with the cognitive construction of the self, and that person's outcomes are shared (Aron et al., 1991; Mashek and Aron, 2004). This expansion helps fulfill the human need to expand one's efficacy. The other person informs who we are, provides new tools for our use, shapes our world view, and affects our perceived costs and benefits. The desire to include the other in the self is a dynamic motivation to pursue a pair bond; and the pair bond itself is an enduring feature of having successfully included the other in the self. The relation between the two constructs is so integrated that in essence, pair-bonding could be described as the inclusion of the other in the self and the inclusion of the other in the self is certainly an example of pair-bonding.

This paper reviews illustrations of the role and application of IOS and contributes to the understanding of the important connection between the two constructs of pair-bonding and IOS. It demonstrates that including the other in the self can in fact predict enduring adult romantic relationships and illustrates significant results of such bonding. Aron et al. (2013)

conducted a comprehensive literature survey that documented previous IOS research. They included studies that highlighted both predictors and outcomes of IOS. Since the publication of the Aron et al. review in 2013, the field of IOS research has continued to broaden (Aron et al., 2013). The following discussion reviews selected studies from the 2013 review and highlights some of the work since then that has expanded and enhanced the understanding of IOS across three categories: measurement, predictors of IOS, and outcomes of IOS.

MEASUREMENT OF INCLUSION OF OTHERS IN THE SELF

To measure the closeness experienced in pair-bonded relationships, Aron et al. (1992) designed the IOS Scale. The IOS Scale features the metaphor of overlapping selves and encapsulates the construct of interconnected selves by presenting seven pairs of overlapping circles with each pair overlapping slightly more than the preceding pair. Respondents select the pair of circles that best portrays their relationship. The original validation of the IOS Scale captured aspects of both *feeling* close and *behaving* close, and correlated strongly with more complex, multi-item measures of closeness and intimacy (Aron et al., 1992).

The IOS Scale is impressively flexible and has been used cross-culturally to study diverse categories of personal relationships (e.g., Uleman et al., 2000; Dalsky et al., 2008). With its pictorial presentation, the IOS Scale presents no language barriers. Further, capitalizing on the availability of technology, a dynamic IOS Scale was created for use in Web-based data collection where a computer mouse can be used to alter the relationship between the two circles, or selves (Le et al., 2007). Although several other measures of closeness, including the implicit me-not-me task (Aron et al., 1991, Study 3), have been used successfully in much research, including to help validate the IOS Scale, the IOS Scale is the most common—and, arguably, the most face-valid—measure of inclusion. And because it is a single item, it is particularly efficient. To date, the paper that originated the IOS Scale has over 3,800 citations.

Adding to previous literature, the most recent comprehensive evaluation of the IOS Scale found it to be a psychologically meaningful and highly reliable measure of the subjective closeness of relationships for a diverse online sample of adults (Gächter et al., 2015).Offering a new strategy for assessing IOS, Castañeda et al. (2015) assessed whether Facebook profiles could be used to measure relationship closeness. They found positive associations between self-reported IOS and the couple's Facebook overlap, which refers to how couple's individual Facebook profiles overlap as measured in shared pictures, friends, and similar "likes." Further, *Facebook* overlap was associated with commitment and relationship investment in ways comparable to self-reported IOS. These findings suggest that overlap in Facebook profiles can be used as an objective indicator of IOS.

Given the pair bond itself is an enduring feature of having successfully included the other in the self, measuring IOS captures depth and breadth of the pair bond.

PREDICTORS OF INCLUDING OTHERS IN THE SELF

In the 2013 review, one study examining what predicts IOS found that self-disclosure was a strong mechanism for creating IOS, demonstrating experimentally that gradually increasing reciprocal self-disclosure with a stranger can create greater IOS (Aron et al., 1997). Another study found that sharing exciting activities—versus boredom—in marriage in year 7 predicted increased satisfaction in year 16, and that changes in IOS mediated this effect (Tsapelas et al., 2009). Yet another theoretically interesting approach to induce inclusion, based on Fredrickson's (2001) broaden and build theory, found that inducing positive affect increases IOS with a close friend (Waugh and Fredrickson, 2006).

Research continues to unpack predictors of IOS. Recent insights regarding humor and attachment avoidance are introduced below.

Humor is a common interpersonal tool that has been the subject of previous research on relationships suggesting it may positively influence the trajectories of social interactions (Storey, 2003; Fraley and Aron, 2004; Wilbur and Campbell, 2011), including IOS. Treger et al. (2013) examined it in regard to how it was associated with closeness as measured by the IOS scale. In two social interaction experiments, the authors examined the association between humor and liking. In both studies, the use of humor was positively associated with liking and closeness. Perceived reciprocal liking and enjoyment of the interaction mediated the association. The findings suggest that humor is a mechanism used to establish connections with others.

Finally, a brief perspective-taking induction preceding couples' unresolved conflict discussions was shown to interact with individual differences in attachment avoidance to influence post-conflict ratings of self-partner overlap. The authors found that the perspective-taking induction buffered the effect of partner—but not one's own—avoidance on self-partner overlap (Bernstein et al., 2015).

The studies highlighted in this section suggest several interesting possible avenues to establish and enhance IOS—and thus pair-bonding—such as: increasing reciprocal self-disclosure, sharing in exciting activities, inducing positive affect, the use of humor, and perspective-taking training.

OUTCOMES OF INCLUDING OTHERS IN THE SELF

Outcomes of IOS were demonstrated in a number of studies included in the 2013 review: the "me/not-me" paradigm illustrated that when another person is included in the self, one's ability to process information about the self on a particular trait is slowed to the extent that the other is dissimilar on that trait (Aron et al., 1991); confusions between self and close others were more likely than confusions between self and non-close others when recalling adjectives previously rated as describing three different targets (Mashek et al., 2003); more use of plural pronouns was correlated with more inclusion (Agnew et al., 1998);

people in relationships perceived themselves as less constrained in their physical nature because they included the other's physical attributes (Burris and Rempel, 2008); individuals processed physical pain experienced by self and a close other the same, but not with a stranger (Cheng et al., 2010); and a close other's success was celebrated, rather than seen as threatening (Gardner et al., 2002).

More recent literature builds on this body of knowledge about the beneficial outcomes of including others in the self. For example, Weinstein et al. (2016) applied principles from self-determination theory to examine whether individual differences in self-determined motivation moderated the effects of higher self-other overlap on partner outcomes. Results showed that when self-determined individuals reported greater self-other overlap, their partners also reported receiving more positive motivational support as well as enhanced commitment. Conversely, when individuals were low in self-determination, partners did not benefit from greater self-other overlap. These results suggest that the benefits of closeness in a romantic relationship are dependent upon one's partner approaching the relationship fully, authentically, and from their own values rather than for extrinsically motivated reasons.

A recent study (Walsh and Neff, 2018) looked at "identity fusion" and its impact on handling conflicts in pair-bonded romantic relationships. Results demonstrated that individuals who perceived greater fusion with their partner (i.e., perceived an equal blending of the personal and partner's self in creating their unique couple identity) exhibited reduced vigilance for relationship threats and enacted more constructive coping responses to relationship conflict. On the other hand, individuals who perceived an imbalanced couple identity (i.e., perceived either their own or their partner's identity as dominant in the couple identity) exhibited fewer of these pro-relationship behaviors. This research provides an important extension to the IOS literature by not just focusing on the amount of overlap between partners, but rather, the different ways selves can be integrated.

While experiences of closeness in romantic relationships have been found to be associated with increased levels of relational well-being and mental health (Reis et al., 2000; Reis and Aron, 2008; Holt-Lunstad et al., 2010), individuals differ in their desire for closeness in a relationship (Mashek and Sherman, 2004). To further examine that variance, a longitudinal survey of partnered individuals measured participants' actual and ideal IOS across three time points. Results demonstrated that optimal levels of relational well-being and mental health existed when individuals had minimal discrepancies between actual and ideal IOS over time, regardless of their actual levels of IOS (Frost and Forrester, 2013). These findings suggest that closeness regulation may be an important mechanism to improve mental health and relational well-being over time, above and beyond promoting closeness itself.

Thai and Lockwood (2015) examined social comparison in the context of a romantic relationship. The authors examined whether individuals respond to comparisons involving romantic partners as they would to comparisons involving the self. Results indicated that, when reminded of their partner's inferiority in a domain, high self-other overlap participants maintained positive global partner perceptions, whereas low overlap participants' global perceptions were negatively affected. These results suggest that perceptions of partners remain robust when we feel a high degree of overlap with them, even when presented with specific evidence that our partners may not be perfect.

Other recent work, however, highlights potential challenges of increased self-other overlap (i.e., IOS). For example, although chronic pain has been linked to poorer psychosocial well-being in the spouse (Schwartz and Slater, 1991), the extent to which partner pain affects spouse sleep had not been researched. Martire et al. (2013) tested the hypothesis that greater daily knee pain would be associated with poorer sleep that evening for the spouse, and that the spouse's sleep quality would be worse in couples who have a closer relationship as measured by the IOS Scale. Results indicated that greater knee pain at the end of the day was associated with spouses' poorer overall sleep quality that night controlling for disturbances in patient sleep; this effect was stronger in couples with a high level of closeness.

In a disturbing application of IOS, Benavidez et al. (2016) examined the effect of closeness between partners in cultures of honor where women, when seen as disgracing their mate, can be violently punished. Endorsement of a "culture of honor," where male partners' or family members' reputations can be tarnished by the acts of the females in the family, contributes to the belief that family honor is tied to female obedience across a variety of moral values. In this study, male participants filled out a measure of cultural honor and closeness to their wife or partner as measured by the IOS. Participants with high levels of both closeness and honor were most aggressive toward a hypothetical moral violation. In sum, within a culture of honor, the closer honor-endorsing men are to women, the more perceived violations by women are met with increased aggression.

In another direction, Slotter et al. (2014) focused on the effect of relationship dissolution on attributes that were attained through the inclusion of the other in the self. They examined factors that predicted whether individuals retain or reject attributes from their self-concept that they had initially gained during a relationship. Results indicated that individuals preserve aspects they had garnered from a former partner in their self-concepts if they had invested greater, versus lesser, psychological, mental, or physical effort to maintain those attributes; however, when these attributes actually conflict with their own previously held beliefs and attitudes, it can be confusing and lead to reduced self-concept clarity upon relationship dissolution. This research suggests that the harder one works to include another's conflicting attributes in one's self-concept, the more vulnerable one's self-concept may be should the relationship end.

The studies in this section illustrate some of the benefits and challenges of a stronger pair bond. For example, those that are more bonded by including more of the other in the self are shown to practice more constructive responses to relationship conflict; to have enhanced commitment when bonded to a self-determined, authentic partner; and to maintain positive global perceptions of partners. Demonstrated challenges associated with stronger bonding include: poorer sleep when one's partner experiences chronic pain, increased aggression within a culture of honor the closer the honor-endorsing male is to the woman, and more difficulty reconciling self-concept upon relationship dissolution.

RECENT THEORETICAL DIRECTIONS

While the research reviewed above examines applications of IOS based on the original theoretical framework, two new theoretical directions hold promise for expanding the understanding and application of IOS as it relates to pair-bonding.

Mattingly et al. (2014) developed a theoretical framework, the two-dimensional model of relational self-change, to better understand how romantic relationships can affect an individual's sense of self, and how those changes are related to relationship functioning. According to the model, self-concept change occurs along two independent dimensions: *direction*—whether the self-concept has lost or gained content, and *valance*—whether the self-concept content is positive or negative. These dimensions create four distinct self-change processes: two that improve self-concept—*self-expansion* (individuals gain positive traits) and *self-pruning* (individuals lose negative traits); and two that degrade self-concept—*self-contraction* (individuals lose positive traits) and *self-adulteration* (individuals gain negative traits). Mattingly et al. (2014) developed a measure of self-concept change and found that the self-concept improvement processes were associated with greater love and relationship quality, while the self-concept degradation processes were associated with more infidelity.

In a further investigation, McIntyre et al. (2015) studied how perceived relationally induced self-concept changes were associated with relationship quality, as well as relational behaviors and motivations. McIntyre et al. (2015) found that increases in self-expansion and self-pruning were associated with greater relationship satisfaction and commitment, while increases in self-contraction and self-adulteration were associated with a subsequent decrease in satisfaction and commitment. In a second study, McIntyre et al. (2015) found that self-expansion and self-pruning were positively associated with relationship maintenance behaviors such as willingness to sacrifice and forgiveness, whereas self-contraction and self-degradation were negatively associated with these outcomes and positively associated with potentially harmful relationship behaviors such as seeking revenge and attention to alternatives. The two-dimensional model suggests that the gains or losses one perceives by including another in oneself have important implications for one's self-concept and the subsequent relationship quality they experience.

In another theoretical innovation, Tomlinson and Aron (2013) extended the IOS model to incorporate one's perception of the extent to which the partner includes oneself in his or her self-concept by introducing a new construct—perceived inclusion of other in the self (IOS-perceived). This model posits that perceived partner satisfaction (i.e., one's belief about how satisfied one's partner is in the relationship) leads to perceptions of partner closeness (i.e., one's belief about how close their partner feels to them, or IOS-perceived), which impacts one's own closeness to the partner (IOS). IOS-perceived was measured with just a slight modification of the original IOS overlapping-circles scale: asking participants to answer as if they were their partner. In two independent studies, Tomlinson and Aron found strong support for the proposed mediational model, emphasizing the importance of measuring specific perceptions of the partner's feelings about satisfaction and closeness.

In the first new theoretical direction discussed above, the two-dimensional model suggests that the gains or losses one perceives when pair-bonded impact one's self-concept and relationship quality. The second illustrates the importance of one's belief of how satisfied one's partner is in the relationship and how close their partner feels to them in engendering closeness and encouraging reciprocal bonding.

CONCLUSION AND FUTURE DIRECTIONS

This article surveyed scholarship on the self-expansion model's principle of IOS as it relates to long-term pair-bonding. The highlighted studies indicated that the constructs of pair-bonding and IOS are interrelated and complementary, as the desire to include the other in the self is a dynamic motivation to pursue a pair bond; and the pair bond itself is an enduring feature of having successfully included the other in the self. This review illustrated the utility of drawing upon IOS research when considering pair-bonding in the context of long-term adult romantic relationships.

When contemplating the future directions of the IOS principle of self-expansion as it relates to pair-bonding, a number of fertile areas present. Although the current review describes the theoretical linkage between IOS and pair-bonding, empirical research should more explicitly evaluate whether motivation for IOS is a major reason for pair-bonding. Additionally, to advance the literature regarding the association between pair-bonding and relationship dissolution, research could expand from break-up scenarios to looking at the effects of a partner's death. This direction would prove interesting and perhaps inform bereavement counseling. It might also prove fruitful to explore IOS as a state rather than just as a trait, examining the differences between short- and long-term pair-bonded relationships. Finally, to further clarify the cognitive function of the bonding process, studies should also examine how IOS (as measured by self-report, implicit measures, and by overlap of neural systems between self and other) correlates with neural systems found for pair-bonding in animals.

AUTHOR CONTRIBUTIONS

BB, DM, and AA contributed to conception and design of the literature review and wrote sections of the manuscript. BB organized the literature review and wrote the first draft of the manuscript. DM and AA assisted with selection of articles. All authors contributed to manuscript revision, read and approved the submitted version.

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The Prairie Vole Model of Pair-Bonding and Its Sensitivity to Addictive Substances

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The prairie vole (*Microtus ochrogaster*) is an extensively studied model for understanding the neural mechanisms underlying social affiliations and pair bonds. With clearly observed face and construct validity, this species offers translational insights into mechanisms involved in intimate relationships in humans. Moreover, the prairie vole model promises to advance our understanding – as well as allow for predictions – of the effects of extraneous factors (not normally encountered in nature) on such relationships. This mini review describes some of the neurobiological mechanisms regulating social affiliation in prairie voles, followed by an overview of the effects of alcohol and other drugs of abuse on formation and maintenance of pair-bonds. Based on available literature, we demonstrate that the effects of such extraneous factors on formation and maintenance of pair-bonds are sex-dependent, as well as dependent on the specific nature of the addictive drug. In turn, the lack of similarities in effects of different addictive substances on pair-bond formation suggests that these substances engage different neurocircuits that may or may not overlap with neurocircuits involved in various social behaviors. This lack of consistency of effects across studied drugs of abuse indicates the need to further examine the effects of individual drugs on affiliative behaviors. We highlight the deficiencies in this field of research, particularly the sparsity of studies on effects of drugs of abuse on the maintenance of established bonds. Future investigations in this field could help design strategies to help afflicted individuals.

Keywords: mating, pair-bond, partner preference, prairie vole, oxytocin, corticotropin releasing factor, alcohol

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INTRODUCTION

Reproduction, whether asexual or sexual, is of the upmost importance to the survival of a species. Consequently, organisms have evolved various mating systems to ensure reproduction. Nevertheless, throughout the animal kingdom, promiscuity reigns supreme. Approximately 95–97% of mammals utilize this mating strategy, while the remaining 3–5% exhibit social monogamy (Lukas and Clutton-Brock, 2013; Johnson and Young, 2015). Because social monogamy does not require sexual exclusivity, this strategy can provide a valuable insight into biological aspects of social attachments.

Research on the prairie vole (*Microtus ochrogaster*) – a socially monogamous rodent species – allowed for characterization of the neurobiological underpinnings of the pair-bond. Moreover, the effects of alternative rewards and addictive substances on pair-bonds can be investigated by utilizing these animals. This review focuses on the prairie vole model of pair-bonding, its translational value to human social attachments, and its sensitivity to the effects of alcohol and drugs of abuse.

PAIR BOND AS THE HALLMARK OF SOCIAL MONOGAMY

Pair-bonds are commonly described as enduring, preferential associations between two sexually mature adults, characterized by selective affiliation, contact, and mating with the partner over a stranger, which is generally called partner preference (PP; Young et al., 2011). Pair-bonded animals also show aggression toward sexual competitors – called "mate-guarding" – and biparental care of offspring (Kleiman, 1977; Buss, 1988; Fraley et al., 2005). These are social behaviors also seen in humans. The occurrence of sociosexual attachments in nearly all human civilizations provides compelling evidence in support of these attachments being intrinsic to human social behavior (Young et al., 2011).

There are physiological and psychological advantages of pair-bonds in humans. Paired individuals live longer than unpaired individuals across all demographic groups (House et al., 1988; Lillard and Waite, 1995). Interestingly, the level of intimacy between two bonded individuals is positively correlated with immune function and cardiovascular health, while it is inversely correlated with depressed mood (Millard et al., 1988; Kiecolt-Glaser and Newton, 2001). Importantly, socially monogamous behaviors appear to be facilitated by distinct and evolutionary conserved neural mechanisms that mediate selective social attachments.

NEUROBIOLOGY OF PAIR BONDING

Dopamine (DA) signaling is implicated in the formation, expression, and maintenance of pair-bonds. Prairie voles display higher densities of DA2 receptors (D2Rs) and decreased expression of DA1 receptors (D1Rs) in the medial prefrontal cortex (mPFC), as well as a lower density of D1Rs in the nucleus accumbens (NAcc), compared to promiscuous meadow voles (Aragona et al., 2006; Smeltzer et al., 2006). Mating increases DA activity and D1R:D2R signaling ratio in the NAcc, facilitating PP formation (Young et al., 2011; Resendez and Aragona, 2013). D2R activation is necessary and sufficient for PP formation in both male and female prairie voles (Gingrich et al., 2000; Aragona et al., 2006). Following formation, bond maintenance is ensured by increased D1R expression in the NAcc (Aragona et al., 2006; Resendez and Aragona, 2013). In addition, DA cells have been found in the bed nucleus of the stria terminalis (BNST) and the medial amygdala (MeA) in the prairie vole but not in the meadow vole (Northcutt et al., 2007). The larger implication of studies in diverse species such as zebra finch and coppery titi monkeys is support for an evolutionarily conserved contribution of these reward and learning pathways to pair-bonding (Bales et al., 2007; Banerjee et al., 2013). Indeed, recent imaging studies point to the associations between levels of D2/3Rs in the ventral striatum and self-reported social attachment (Caravaggio et al., 2017), and to increased DA activity in the MeA during bonding in humans (Atzil et al., 2017).

Oxytocin (Oxt) is a conserved nonapeptide mediating species-specific social and maternal behaviors (Pedersen and Prange, 1979; Ferris et al., 1984; Kendrick et al., 1987; Argiolas and Melis, 2005). The distribution of Oxt receptors (Oxtr) varies within and across species (Anacker and Beery, 2013; Albers, 2015). Specifically, socially monogamous voles display higher densities of Oxtr in the BNST, mPFC, and NAcc but lower levels of Oxtr binding in the ventromedial hypothalamus, LS, and anterior cortical amygdala (Insel and Shapiro, 1992; Young et al., 1996; Smeltzer et al., 2006). Oxtr expression within mesolimbic pathways is critical for pair-bonding (Young et al., 2011). Furthermore, the Oxt and DA systems interact in their functions related to pair-bonding (Liu and Wang, 2003). In humans, Oxt and Oxtr are also closely associated with social behaviors (Ebstein et al., 2009; Heinrichs et al., 2009; Meyer-Lindenberg et al., 2011). Perhaps most interestingly, Oxtr gene variants are associated with relationship status (Walum et al., 2008, 2012), and Oxt levels within blood plasma can predict success rates in romantic relationships (Schneiderman et al., 2012).

Arginine vasopressin (AVP), a peptide similar to Oxt, is also implicated in the regulation of social bonding. AVP receptor 1a (AVPR1a) expression is higher in the ventral pallidum (VP) and LS in monogamous versus promiscuous vole species (Nair and Young, 2006), and AVP signaling in VP and LS is causally linked to PP (Liu et al., 2001; Lim et al., 2004; Donaldson et al., 2010). On the other hand, mate-guarding in prairie voles is dependent on AVPR1a signaling in the anterior hypothalamus (Gobrogge et al., 2009). AVPR1a in the retrosplenial cortex is important for the regulation of monogamous behaviors in wild prairie voles (Okhovat et al., 2015; Ophir, 2017). In agreement with the translational value of these findings, AVPR1 polymorphisms are associated with effects of childhood adversity on social interactions in adulthood (Liu et al., 2015). Moreover, administration of AVP increased empathic concerns and risky cooperative behaviors in humans (Tabak et al., 2015; Brunnlieb et al., 2016).

Pair-bonding also involves the corticotropin releasing factor (CRF) receptor system. Monogamous voles display lesser levels of CRFR1 and greater levels of CRFR2 binding within the NAcc (Lim et al., 2005, 2006). Administration of CRF into either the cerebral ventricles or intra-NAcc promoted PP formation in male prairie voles, and effects are prevented by concurrent administration of either a CRFR1 or CRFR2 antagonist (DeVries et al., 2002; Lim et al., 2007). These effects involve either CRF or urocortin 1, since the latter peptide has higher affinity than CRF to these receptors. Indeed, urocortin 1 also shows higher levels of expression in the centrally projecting Edinger-Westphal nucleus (EWcp) in promiscuous versus monogamous vole species (Lim et al., 2005, 2006). The contributions of the CRF system to social attachment are translationally relevant as human polymorphisms in the CRHR1 gene (encoding CRFR1) moderate loneliness in older adults (Chou et al., 2014) and effects of early life stress on emotional empathy (Grimm et al., 2017). Thus, collective neuroplastic abilities of these evolutionarily conserved and connected systems are responsible for the formation and maintenance of the pair-bond.

EFFECTS OF ADDICTIVE SUBSTANCES ON SOCIAL BONDING IN HUMANS

Addictive substances profoundly affect human social behavior. Many addictive substances are taken in social circumstances and are often expected to promote social bonding. However, drug abuse is associated with deleterious effects on social relationships; in fact, alcohol and drug abuse are the third most cited reason for divorce in the United States (Amato and Previti, 2003). Because of the difficulties in obtaining data on the use of illicit drugs, researchers often combine data from several drugs to increase the statistical power. These studies consistently point to the negative association between drug abuse and social bonding, relationship stability, and relationship satisfaction (Dull, 1984; Fals-Stewart et al., 1999). This association is much better followed for addictive substances that are used legally, like alcohol.

While confirming the negative effect of heavy alcohol use on various measures of social bonding, research also identified differences between modes of alcohol drinking within couples. Specifically, couples in which only one spouse drinks heavily (discordant) are less stable than couples in which both spouses drink heavily (concordant) or abstinent couples, while concordant couples are significantly more stable than discordant drinking couples and may be just as stable as abstinent couples (Marshal, 2003; Ostermann et al., 2005; Torvik et al., 2013; Leonard et al., 2014). Additionally, rates of marital dissatisfaction and separation are higher among couples when there is a difference in alcohol consumption between partners (Mudar et al., 2001; Homish and Leonard, 2007; Homish et al., 2009). Interestingly, while this difference in rates of separation is observed in relation to alcohol, neither concordant nor discordant tobacco or marijuana use is associated with increased divorce (Leonard et al., 2014). The latter data indicate that while addictive substances have strong negative effects on the stability of human bonds, there are differences between specific drugs that should be examined. Intriguingly, while socioeconomic factors impact the stability of a marriage, these factors do not moderate effects of addictive substances on marital stability, suggesting involvement of biological factors (Ribar and Kenkel, 1994; Leonard et al., 2014).

PRAIRIE VOLES AS MODEL OF EFFECTS OF ADDICTIVE SUBSTANCES ON PAIR BONDING

While epidemiological research on associations between the use of specific drugs of abuse and social effects is being increasingly performed, assessing causal relations between factors requires the use of animal models. Traditional laboratory animals (i.e., mice and rats) are not very suitable for these experiments because they do not display social monogamy. By contrast, prairie voles offer a well-established model of pair bonding and affiliative behaviors. In addition, prairie voles freely prefer alcohol solutions over water (Anacker et al., 2011) and can also consume solutions of methamphetamine (Hostetler et al., 2016).

Early work investigating the influence of social factors on rewarding properties of drugs showed that pair-bond formation reduces amphetamine (AMPH) seeking as evaluated by conditioned place preference (CPP; Liu et al., 2010, 2011). CPP pairs a context with a stimulus, in this case a drug, and assesses preference for the paired context through comparison of time spent in the paired versus alternative, non-paired context. CPP does not assess effects of voluntary exposure to a drug and is accompanied by stress of drug administration. Therefore, subsequent studies used voluntary modes of self-administration, focusing on alcohol consumption. These studies demonstrated existence of social facilitation and social inhibition of alcohol drinking, as well as effects of social hierarchies on alcohol drinking (Anacker et al., 2011, 2014b; Hostetler et al., 2012; Hostetler and Ryabinin, 2014) – both increasing and decreasing alcohol consumption dependent on a number of contextual variables. These first experiments were performed in same-sex pairs of prairie voles. More recent studies observed facilitation of alcohol consumption in pair-bonded male-female pairs of prairie voles (Walcott and Ryabinin, 2017, 2019). The social facilitation of drug intake was observed for alcohol, but not for methamphetamine (Hostetler et al., 2016), highlighting differences in the effects of social environment on actions of these addictive substances.

While the latter studies highlighted the effects of pair-bond formation on consumption of addictive substances, they did not explain the disruptive effects of substance abuse on social bonds. A different series of studies specifically tested whether such disruptive effects observed in humans could be replicated in prairie voles (**Figure 1**). An early report demonstrated that administration of morphine attenuated huddling of male-female pairs (Shapiro et al., 1989). This effect was observed with a relatively high dose of morphine (10 mg/kg) also decreasing locomotor activity. The study also did not assess behavior of males and females separately. Nevertheless, it suggested that drugs of abuse can have inhibitory effects on processes indicative of pair-bonding. Subsequent studies showed that injection of AMPH prior to cohabitation could enhance pair-bond formation in male prairie voles and that this effect is dependent on D1R activation (Curtis and Wang, 2007). On the other hand, repeated (three times) AMPH administration in male prairie voles resulted in increased aggression toward female voles, an effect dependent on AVPR1a in the anterior hypothalamus (Gobrogge et al., 2009). Such repeated treatment disrupted formation of PP in male prairie voles. Blocking D1 receptors in the NAcc in this study rescued PP (Liu et al., 2010). Repeated AMPH was also shown to disrupt PP formation in female prairie voles at doses lower than in males, and administration of Oxt into the mPFC restored PP in these females (Young et al., 2014). The apparent contradiction between the first studies showing AMPH inducing PP and the subsequent studies showing inhibition of PP could be due to the fact that in the early study, AMPH was administered acutely and immediately prior to cohabitation, whereas in the subsequent studies, cohabitation happened at least 24 h after the last of repeated injections.

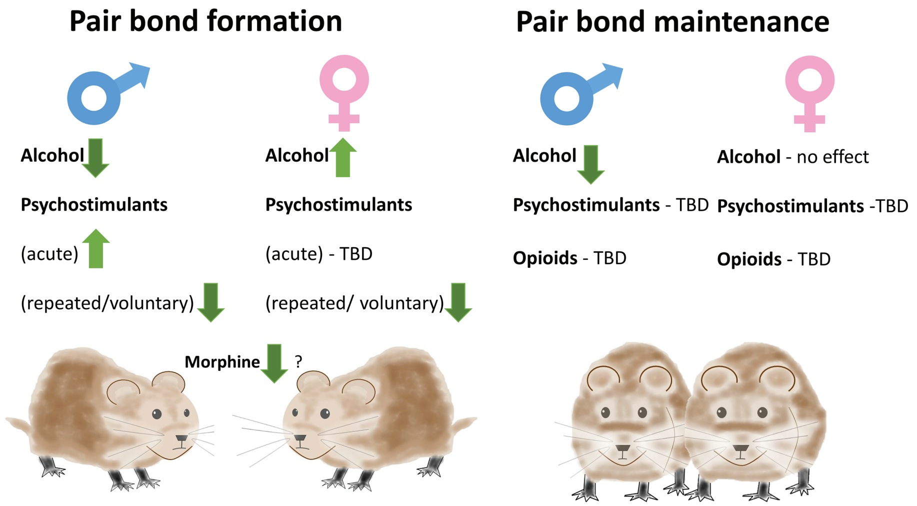

FIGURE 1 | Effects of addictive substances on pair-bonding in prairie voles. Alcohol consumption inhibits pair-bond formation in males but facilitates it in females. Amphetamine administration can either enhance or inhibit pair-bond formation in males depending on timing of administration. Repeated amphetamine administration and methamphetamine drinking inhibit pair-bond formation in both males and females when the exposure occurs 24 h prior to testing partner preference. Morphine can inhibit huddling in male-female pairs. Depending on the partner's drinking status, alcohol consumption can inhibit pair-bond maintenance in males. Alcohol consumption does not have a significant effect on pair-bond maintenance in females.

In the studies described above, AMPH was administered by an experimenter. To alleviate the effect of experimenter-induced stress, studies in our laboratory implemented voluntary consumption of drugs to assess their effects on pair-bonding. In these studies, alcohol produced paradoxical sex-dependent effects on pair-bond formation. Alcohol consumption during cohabitation disrupted PP formation in male prairie voles, but facilitated it in females (Anacker et al., 2014a). A number of neural correlates accompanied the differences in PP, including sex-specific changes in the arcuate nucleus, EWcp, MeA, and BNST, suggesting complexity of actions through which alcohol affects pair-bonds. However, their contribution to regulation of pair-bond formation was not causally evaluated. Subsequent experiments mimicked earlier studies on effects of AMPH, but used animals that were voluntarily drinking a solution of methamphetamine during 3 days of cohabitation 24 h before the PP. Similar to the AMPH injection studies, methamphetamine decreased PP formation in both males and females (Hostetler et al., 2016). This effect was accompanied by a decrease in Oxt immunoreactivity in the paraventricular nucleus of hypothalamus (PVN).

There is an obvious difference between most of the above described experiments testing effects of psychostimulants and alcohol on pair-bonding. Alcohol was self-administered just prior to the PP test, whereas in all but one experiment with psychostimulants, there was at least 24 h after the last drug exposure. The alcohol and psychostimulant studies could be comparing acute effects versus effects of withdrawal. Future studies should address this discrepancy. Nevertheless, it is worth noting that one study that tested effects of acute AMPH in male prairie voles found induction of PP (Curtis and Wang, 2007), whereas acute alcohol consumption inhibited PP in male prairie voles (Anacker et al., 2014a), indicating differential effects of these addictive substances on pair-bonding.

The studies above showed that different drugs can have varied effects on the formation of pair-bonds. However, while substance abuse may delay the formation of social bonds, it seems more clinically important to assess its effects on the stability of already established bonds. Moreover, studies in prairie voles indicate that maintenance of the pair-bond requires additional mechanisms beyond those involved in pair-bond formation (e.g., aversion to non-partner animals; Aragona et al., 2006; Resendez and Aragona, 2013). Studies modeling the effects of drugs of abuse on pair-bond maintenance have only been performed recently and only tested the effects of alcohol. These studies show disruption of the established pair-bonds in male prairie voles – as evidenced by decreased PP – when only the male consumes alcohol, but no disruption when both male and female consume alcohol (Walcott and Ryabinin, 2017). Conversely, no disruption of the established pair-bond was seen in females – irrespective of whether the partner consumed alcohol (Walcott and Ryabinin, 2019). Alcohol consumption decreased Oxt in the PVN of males and females regardless of whether bond was disrupted by alcohol or not (Walcott and Ryabinin, 2019). Interestingly, only males demonstrated an increase in immunoreactivity of the activity marker FosB in the periaqueductal gray (PAG) following discordant drinking – suggesting this area may be involved in mediating the effects of discordant drinking on pair-bond maintenance or sensitive to the conditions of discordant drinking (Walcott and Ryabinin, 2017). The PAG is involved in defensive behaviors and romantic love, besides other functions (Depaulis et al., 1992; Acevedo et al., 2012), and needs to be explored in greater detail. We are not aware of studies testing effects of other drugs of abuse on pair-bond maintenance.

The results of these prairie vole studies complement results of the limited epidemiological studies showing that discordant, but not concordant, alcohol consumption is associated with instability of established social bonds. This is important, as the epidemiological studies only assess associations, but not causality of the effects of alcohol. On the other hand, these results also partly contradict epidemiological results in that discordant drinking in the epidemiological studies was associated with instability of social bonds in both males and females. A number of possible explanations for this contradiction have been put forth (Walcott and Ryabinin, 2019). Perhaps most notably, the vole experiments did not assess the same behavior(s) as the human studies on separations; for example, they did not examine actions of the non-intoxicated subject in the PP test. The experimental design of the vole studies contrasts with the epidemiological situation where the initiator of the separation is most likely the low-consuming individual and not the heavy-drinking spouse. Further behavioral data from both preclinical and clinical studies are required to understand the effects of alcohol on pair-bonds; for instance, is the non-intoxicated partner not interacting with the partner consuming the drug, vice versa or mutual?

The involvement of similar neural substrates in pair bonding and addiction has led a number of researchers to suggest that pair-bonding, or even love, is a form of addiction (Insel, 2003; Burkett and Young, 2012). However, we have argued that this similarity could be superficial. Instead, different addictive drugs can "hijack" neurocircuits that are either involved or not involved in various specific social behaviors (Hostetler and Ryabinin, 2012). As a result, different addictive drugs, or even different phases of actions of the same drug (e.g., intoxication versus withdrawal) can have different directions of effects on pair-bonding. Examples of these effects provided in this review (**Figure 1**) serve as evidence confirming this idea.

Looking forward, what is clearly missing in this literature is a careful examination of effects of different drugs of abuse on maintenance of pair-bonds. So far, only effects of alcohol on this phenomenon have been assessed. Studies on the effects of other drugs of abuse on maintenance of established pair bonds could suggest strategies to help afflicted individuals. Importantly, the prairie vole model is an excellent animal model allowing such future studies.

AUTHOR CONTRIBUTIONS

SP performed the literature search, composition, and writing of the manuscript. AR contributed to writing the manuscript.

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Evolutionary Mismatch in Mating

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Evolutionary mismatch concepts are being fruitfully employed in a number of research domains, including medicine, health, and human cognition and behavior to generate novel hypotheses and better understand existing findings. We contend that research on human mating will benefit from explicitly addressing both the evolutionary mismatch of the people we study and the evolutionary mismatch of people conducting the research. We identified nine mismatch characteristics important to the study of human mating and reviewed the literature related to each of these characteristics. Many of the people we study are: exposed to social media, in temporary relationships, relocatable, autonomous in their mating decisions, nulliparous, in groups that are socially segmented, in an educational setting, confronted with lots of options, and young. We applied mismatch concepts to each characteristic to illustrate the importance of incorporating mismatch into this research area. Our aim in this paper is not to identify all potential mismatch effects in mating research, nor to challenge or disqualify existing data. Rather, we demonstrate principled ways of thinking about evolutionary mismatch in order to propel progress in mating research. We show how attending to the potential effects of mismatch can help us refine our theoretical and methodological approaches and deepen our understanding of existing patterns in the empirical record. We conclude with specific recommendations about how to include consideration of evolutionary mismatch into research on human mating.

Keywords: mating, evolutionary mismatch, evolutionary psychology, attraction, relationships

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INTRODUCTION

Evolutionary mismatch is the idea that physiological and psychological adaptations operate in environments that differ meaningfully from the environments in response to which they originally evolved (e.g., Tooby and Cosmides, 1990; Nesse and Williams, 1994). Mismatch concepts have been addressed across a number of domains, including medicine, health, and human cognition and behavior. Our goal is to explicitly address theorizing about mismatch in one particular domain of human psychology and behavior: human mating. In this paper, we focus on analyzing the ways in which many of the people we study, and we as researchers, embody mismatched characteristics. We consider how sample and researcher mismatch can influence the generation of our hypotheses, the design of our studies, the interpretations of our findings, and ultimately our understanding of human nature. We conclude by offering recommendations for addressing and incorporating mismatch into research on human mating from an evolutionary perspective.

Why Mating Research?

Evolutionary mismatch in research on human mating deserves analysis for three reasons. First, the enterprise of studying human mating from an evolutionary perspective is a research success story. Rigorous application of evolutionary theory to understanding mating cognition and behavior began in the 1980s and has produced an impressive body of work over the past three decades. Not only has studying human mating from an evolutionary perspective provided a foundational framework through which to understand existing research, it has generated knowledge on a host of psychological and behavioral phenomena previously unstudied or poorly understood – including mate selection criteria (Buss, 1989; Kenrick et al., 1990), sexual strategies (Gangestad and Simpson, 1990; Buss and Schmitt, 1993), mate attraction tactics (Thornhill and Gangestad, 1994; Schmitt and Buss, 1996), tactics of mate retention (Flinn, 1988; Buss and Shackelford, 1997), mate poaching (Schmitt, 2004), derogation of competitors (Buss and Dedden, 1990), jealousy-inducing qualities of mating rivals (Buss, 2013a,b), and many others (Symons, 1979; Buss, 2013a,b). The broad focus on human mating adaptations within the evolutionary social sciences is warranted. Reproduction is the currency of evolution, and successful reproduction in sexually reproducing species requires successful mating. Natural selection, therefore, will have profoundly shaped the mating psychology of all species, including humans. And because differential reproductive success is the force that drives evolution, adaptations designed to increase mating success have wide-ranging effects on behavior in many other domains, including intrasexual competition (Buss, 1988), aggression (Wilson and Daly, 1985), status-striving (Turke and Betzig, 1985; Low, 1989), and parent-offspring conflict (Daly and Wilson, 1999). The continued success of the evolutionary mating research program requires that researchers remain critical assessors of our own work. Such assessment is necessary to shape future research and to bolster the validity of existing work. Analysis of the evolutionary mismatch of the populations and samples we study provides one avenue of critical assessment.

Second, much of the existing research on human mating has been conducted on people who are likely to be mismatched from ancestral environments. This is expected, as the vast majority of living humans reside in environments that differ substantially from the likely range of conditions experienced by our ancestors (Tooby and Cosmides, 1990; Foley, 1995). Even people living in traditional cultures, such as modern foraging or horticultural populations, are living in conditions that are probably mismatched from ancestral environments. Changes in land ownership, migration patterns, trade, integration in wage markets, and access to modern technologies ranging from shotguns and chainsaws, to birth control and vaccines, to computers and the internet, have all impacted the ways in which people in modern small-scale societies live, thrive, and survive (Marlowe, 2010; Hill and Hurtado, 2017). However, there is utility in testing adaptationist hypotheses in different environments, and specifically in those environments that are more similar in important ways to likely ancestral environments, particularly in features such as group size and mobility, subsistence and fertility patterns, and the interdependence of close kin for survival (Lee and DeVore, 2017).

Pollet and Saxton (2019) empirically examined the diversity of samples described in papers published in the 2015–2016 volumes of *Evolution and Human Behavior* and *Evolutionary Psychology*, two of the leading journals that publish research on human behavior and psychology from an evolutionary perspective. They found that the majority of samples were online or student samples, and 81% of the samples came from Western cultures. Although these journals include studies on topics outside of human mating, the findings from this study support the conclusion that the preponderance of the data used to test hypotheses about human mating adaptations is derived from people living in environments that dramatically differ from the likely range of ancestral environments that shaped the very adaptations we are investigating.

Analyses of sample diversity must rely on demographic information researchers report in their published papers (e.g., participant nationality). However, researchers can better assess mismatch by identifying social and environmental characteristics that are likely to comprise meaningful mismatch. Greater specificity of mismatched characteristics allows a researcher to assess how those characteristics may or may not act as input into our evolved information-processing mechanisms. From there, a researcher can generate predictions about how the mismatched characteristic influences mechanism output, furthering our understanding of the underlying design. In this paper, we highlight nine specific characteristics of evolutionary mismatch identified by an *a priori* theoretical analysis that are especially relevant to the study of human mating. In reference to Henrich et al. (2010) work highlighting the non-representativeness (or WEIRDness: Western, Educated, Industrialized, Rich, Democratic-ness) of subjects in studies on human psychology and behavior, we arranged our characteristics into a useful acronym that modifies theirs- STRANGELY WEIRD. Our samples are often characterized by people who interact with Social media, engage in Temporary relationships, can Relocate with relative ease, have Autonomy in mate choice, are Nulliparous, experience social Group segmentation, are being tested in an Educational setting, have Lots of options, and are Young adults. Each of these characteristics represents a theoretically relevant divergence from the likely ancestral conditions under which human mating psychology was shaped by natural selection. Populations were small, the available pool of potential mates even smaller, some mate choice was heavily influenced by third-party preferences, and 20-year-olds were experienced parents (Coe and Steadman, 1995; Marlowe, 2005; Walker et al., 2011). This is by no means an exhaustive list of the domains of mating-relevant evolutionary mismatch. We focused on these characteristics because they: (1) are particularly important to the operation of human mating adaptations and, (2) provide useful examples that demonstrate the value of thinking about the implications of mismatch.

Third, because researchers who study human mating from an evolutionary perspective are themselves people who are mismatched, recognizing and evaluating mismatch may be particularly tricky. Studying psychological adaptations is inherently challenging, ironically, because of the design of the mind. The output of psychological mechanisms includes representing information about other people, ourselves, and our environment in ancestrally fitness-beneficial ways. Such representations are not tailored to provide an accurate sense of the underlying mechanisms regulating behavior and the structure of the mind (this argument has been applied to personality science, Lukaszewski, 2019). That the output of researchers' own evolved psychology does not function to "carve nature at its joints" adds to the challenge of conducting research from an evolutionary perspective. Certain cognitive biases owing to this ancestral design, including essentialist beliefs and the appeal of teleological explanations, make engaging in an adaptationist research enterprise difficult (Tooby and Cosmides, 1990; Shtulman and Schulz, 2008). The potentially misleading effects of adaptive biases in perception and interpretation are compounded by the fact that our perspectives on human nature are ontogenetically shaped and continuously updated in the same mismatched environment in which we develop hypotheses and collect data (Fessler, 2010). Evolutionary behavioral scientists, like scientists in other fields, rely on two approaches to hypothesis generation. The theory-driven "top-down" approach consists of using existing theory to develop hypotheses about expected patterns of psychological responses or behavior. In contrast, the observation-driven, "bottom-up" approach begins with observations about patterns of psychological responses or behavior that are interpreted using existing theoretical frameworks and then used to derive novel predictions. When researchers employ this sort of inductive reasoning, they are necessarily relying on observations that occurred in mismatched circumstances. This is a critical part of any scientific endeavor, and is often the starting point for discovering novel features of human cognition and behavior. But these observations may lead researchers to draw erroneous conclusions about underlying universal design of human psychology. We hope this paper will serve as a model for explicitly considering mismatch in the process of hypothesis generation, study design, and data interpretation.

Mismatch in Mind

Our approach to addressing mismatch is derived from the evolutionary psychologist's model of the mind. To an evolutionary psychologist, the mind is a collection of functionally specialized information processing devices, also called evolved psychological mechanisms or psychological adaptations (Cosmides and Tooby, 1995). Each of these devices exists as it does now because, throughout its evolutionary history, it was successful in capturing some information in the environment and processing that information into affective, cognitive, or behavioral outputs that were tributary to solving some recurrent adaptive problem. Adaptive problems are recurrent obstacles to organisms' ability to survive and reproduce, and the identification and analysis of adaptive problems is fundamental to studying evolved psychological mechanisms. Throughout human evolution, psychological mechanism variants that more effectively captured relevant environmental information, processed it according to more efficient decision rules, or produced more appropriate behavioral outputs would have more efficiently solved adaptive problems and would thereby more reliably cause the reproduction of the genes that contributed to their development. Iterated over generations, this selection process crafted in us suites of information processing systems that are improbably well-designed to solve the various reproductive problems that repeatedly confronted our ancestors. The job of the evolutionary psychologist is to recover this improbable design: to map, for any given psychological system, its inputs, decision rules, and outputs, collectively referred to as "design features".

In one sense, this job is environment-agnostic. A complete description of a psychology will extend beyond the description of behavior in context (e.g., "bundle when cold") and into the information processing rules that are invariant across contexts (e.g., "track current temperature in relation to ideal set point and motivate heating or cooling behaviors in response to deviation"). Simply put, if some observation varies systematically with context, it is not design *per se*, but rather the result of design. The aim, therefore, of evolutionary psychology, is not so much to map behaviors across contexts – or worse, to determine the "correct" response under the "right" conditions – but rather to elucidate, by carefully engineering available contexts, the invariant information processing design of the mind. In the same way that one does not need to see an airplane in the air to understand that it is designed for flying (its engines for thrust, its wings for flight), one does not need to see the mind under ancestral conditions to understand its many functions.

But in another very real sense, this fact also makes the environment paramount. Although evolutionary psychologists seek to understand the invariant design of the mind, the mind is nonetheless necessarily observed in a context. And that context will constrain the observations available to researchers on which to infer design. Observing the mind in just a single context – especially naïve to the mismatch between that context and an adaptations' evolutionary history – will likely yield limited inferences. What appears like invariant design in one context may be revealed to be just one of many subroutines when observed in another; seemingly bad design could very well be good design operating under unusual conditions. An evolutionary psychologist seeking to understand the evolved design of some piece of the mind must always consider three things: (1) the adaptive problem the adaptation was designed to solve, (2) the hypothesized information processing designs that would be improbably efficient at solving this problem, and (3) the predicted ways in which this design would interact with the specific environmental contexts available to the researcher to yield empirical observations. Ignoring any of these three processes will lead a researcher to systematically flawed inferences, especially in cases where the environments in which a researcher does their science differ substantially from the environments that generated the adaptive problem in question – that is, in cases of evolutionary mismatch.

ANALYSIS OF THE STRANGELY CHARACTERISTICS

We are not the first to discuss evolutionary mismatch in the context of mating-related adaptations. For example, Symons's (1979) foundational work, *The Evolution of Human Sexuality,* included discussion of mismatched features of modern environments, such as pornography, sperm banks, freedom from parental influences, and potentially endless options for mates. Our goal is to build on existing research and theory that address mismatch and introduce general principles for thinking about mismatched characteristics within the domain of mating adaptations. Armed with insights gleaned from explicit consideration of mismatch related to the characteristics discussed here, we hope researchers will be better equipped to consider the implications of mismatch related to other characteristics and adaptations not described in this paper. In the following subsections, we expand on how each of the STRANGELY characteristics describes an instance of mismatch, review literature relevant to each characteristic, analyze how these characteristics may interact with our evolved psychological mechanisms, and demonstrate how researchers can incorporate consideration of these characteristics into their work. Because there is overlap between some characteristics (e.g., high rates of relocatability and social media increase the number of mate options; participants found in an educational setting are typically young) we focused on ideas unique to each characteristic in order to model different ways of thinking about mismatch and evolved mating psychology.

Social Media

Social media, including social networking platforms such as Facebook and Instagram as well as dating platforms such as Match.com and Tinder, is a novel feature of our environment that can serve as a delivery system for cues that mimic ancestral input and affect many mating-related mechanisms. Because social media exposes people to large amounts of information in short periods of time- a user can swipe through dozens of images in minutes- it can amplify input to psychological mechanisms, especially visual input, at unparalleled levels. Interacting with people on social media, especially on platforms designed for finding mates, can provide a person with an even larger number of mate options, across a greater geographical distance, in a setting with greater anonymity than ever before. Ancestral humans residing in small groups with limited geographic mobility would have encountered, perhaps, a few dozen potential mates in their lifetime (Marlowe, 2005). Social media exposes modern humans to visual images of hundreds within a few days and many thousands over time. Importantly, even if social media does not actually alter something about a person's real mating ecology- for example, they may never actually meet the person with whom they've been chatting who lives 1,000 miles away, let alone have any reproductive opportunities with that person- such cues may alter *perceptions* in ways that affect decision-making and behavior. This consideration is important both when we study online dating and mating behavior in the context of the internet, but also when we study people who interact regularly with social media.

Social media may also indirectly affect mating mechanisms by influencing self-assessment and the outputs of other psychological mechanisms, such as those designed to track status hierarchies (Wilson and Daly, 1985; Lukaszewski et al., 2016). Social networking platforms expose people to others that they may perceive as part of their social group, either as potential options for mates or competitors. Furthermore, they are exposed to others' curated versions of themselves, designed to strategically present themselves in idealized ways (Rui and Stefanone, 2013). Self-comparison to such inaccurate portrayals may influence self-perceptions, including self-perceived attractiveness and mate value (roughly, their overall desirability in a pool of mates), which in-turn influence mating strategies. For example, men higher in self-perceived mate value score higher on measures of sociosexuality, indicating that they are more inclined toward casual sex (Clark, 2006). Self-perceived mate value is also associated with mate preferences- both men and women who are higher in self-perceived mate value place greater importance on desirable traits in potential mates, presumably because they are in a position to attract high quality partners (e.g., Buss and Shackelford, 2008; Burriss et al., 2011). Relatedly, self-perceived mate value discrepancies between a person and their partner impact mate retention tactics, relationship satisfaction, and shame in response to committing relationship transgressions (e.g., Conroy-Beam et al., 2016; Sela et al., 2017; Goetz and Maria, 2019). Thus, adaptations that regulate our self-perceived mate value, perceptions of others mate value, and our self-perceived relative standing on traits that people value in mates may be influenced by exposure to social media.

Social media usage is also positively related to anxiety and depression, and negatively related to self-esteem in adolescents (Woods and Scott, 2016). Researchers have demonstrated the same negative relationship between social media usage and self-esteem in adults, and have demonstrated that negative self-evaluations are a consequence of engaging in social comparison to people observed via social media (Vogel et al., 2014). Anxiety, depression, and self-esteem influence behavior across different types of social interactions, including romantic and sexual relationships (e.g., Shrier et al., 2001). Thus, social media exposure may affect mating outcomes indirectly through its effects on well-being.

Finally, social media provides an evolutionarily novel method through which people initiate and maintain romantic and sexual relationships- both on platforms designed for this purpose (e.g., Tinder) and on platforms with broader social networking functions. Our mate assessment mechanisms were calibrated in an environment where we evaluated potential mates in person, using the full array of cues available to us from *in vivo* interactions, observations, and third-party reports from trusted (and sometimes unreliable) sources. The information provided in an online environment is comparatively impoverished. Not only do evaluators have less information available to them- there are no scent or chemical cues, for example- but the information they do have is either declarative, or the product of selective, and sometimes deceptive, self-presentation (e.g., Toma et al., 2008).

Do mating adaptations functionally assess the information about potential mates provided online as unreliable? Or in the absence of the full of array of cues to which our adaptations evolved to be sensitive, is the weak information provided online or through an app given greater weight because it is the only information available to the evaluator? Explicit mismatch framing generates these sorts of questions, and influences how we interpret findings from studies of mate selection and relationship initiation that occurs via social media platforms.

Temporary Relationships

Evolutionary theorizing on human mating has provided a cogent framework through which to understand the variety of sexual strategies that humans pursue (Buss and Schmitt, 1993; Buss, 2013a,b). There is strong theoretical and empirical evidence that humans have engaged in committed pair-bonds across time and cultures, as well as other types of sexual and romantic relationships that vary in commitment, expectations, and time-frame (Greiling and Buss, 2000; Pillsworth and Haselton, 2006; Conroy-Beam et al., 2015; Scelza and Prall, 2018). Temporary relationships as a theoretical construct are not an example of mismatch. However, the mismatched context in which STRANGELY WEIRD people's short-term mating adaptations operate deserves consideration. One key element of this context to consider is the degree of anonymity. STRANGELY WEIRD people who live in large societies can engage in sexual relationships with virtual strangers and, if they desire, easily never interact with that sexual partner again – a significant departure from the social environments in which our ancestors lived (Krasnow et al., 2013).

There are important hypothesized sex differences in the design of men's and women's short-term mating mechanism (Buss and Schmitt, 1993). In a 9-month period, an ancestral (and modern) woman could get pregnant once, compared to an ancestral man who could have produced dozens of offspring, only limited by the number of fertile women to whom he could gain sexual access. Researchers have hypothesized that men evolved a number of short-term mating adaptations as a consequence, including desire for sex with a variety of women (Symons, 1979); lowering of standards for sexual partners compared to long-term mates (Kenrick et al., 1990), and a desire to have sex sooner than women desire after first meeting a mate (Buss and Schmitt, 1993). These short-term mating adaptations are now operating in an environment with unprecedented anonymity and potential options. Male university students in particular are surrounded by many women displaying cues to youth and fertility, key determinants of judgments of female attractiveness (Kenrick and Keefe, 1992; Li et al., 2002). The combination of these cues- anonymity, many fertile options- may act as a supernormal stimulus, triggering men to pursue short-term mating strategies more strongly than they would have ancestrally. One benefit to researchers is that this makes university men a useful population to study the design of short-term mating adaptations.

Although ancestral women would not have accrued the same fitness benefits by pursuing many sexual partners as men did, researchers have hypothesized that there were likely other fitness benefits to short-term mating that shaped the design of women's short-term mating adaptations (Greiling and Buss, 2000; Pillsworth and Haselton, 2006; Sacco et al., 2012). Women may have gained resources, such as food, protection, or status through short-term sexual relationships. Genetic benefits for offspring are another possible benefit. Additionally, some of the benefits of engaging in short-term mating may have been linked to long-term mating. Short-term mating could have allowed a woman to assess new potential partners, either because she did not currently have one or was considering leaving her current partner; could have helped her eject her current mate or switch to a better mate (Buss et al., 2017); could have helped her clarify her long-term mate preferences and practice her mate attraction skills; or could have been used as a tactic to manipulate her current mate into increasing commitment.

These differences in men's and women's short-term mating adaptations already set the stage for sexual conflict. However, we hypothesize that the mismatched environment of STRANGELY WEIRD people increases the likelihood and magnitude of some forms of sexual conflict. Some men primed by the mismatched environment may sexually pursue women to the point of harassment- or worse, they may employ coercive and exploitative strategies (Goetz et al., 2012). Men who are unsuccessful in gaining short-term sexual access are not only operating in an environment that strongly triggers short-term mating motivation, but they also may be attuned to others' relatively greater success. Incels are a subgroup of men who define themselves by their inability to gain sexual access to women (incel = "involuntarily celibate"). Incels express an entitlement to sex and resent that they have been denied, display extreme misogyny toward women, and advocate for violence against women and against men who are sexually successful (Ging, 2017). We hypothesize that elements of mismatch fuel the rise of such subgroups- in addition to being primed to pursue short-term mating, incels can use online forums to discuss their ideas and develop as a group with complete anonymity.

Women's short-term mating adaptations can also be assessed through the lens of mismatch- particularly adaptations that are hypothesized to link short-term mating motivation to long-term mating goals. Prior to contraception, engaging in a temporary sexual relationship would have been reliably linked to conception. This could motivate a woman to attempt to convert a short-term mate into an investing mate, particularly in an environment where a woman's family and kin are nearby and could exert influence to ensure a man invests and commits. Other potential benefits to short-term mating in women, such as obtaining high-quality fish, meat, or other resources, switching to a new mate, or maintaining a potential back-up mate, are less likely to be realized if a woman's short-term mate can more easily leave or avoid committing- which characterizes relocatable men in large societies with increased anonymity. If women's short-term mating adaptations are blind to these novel features of our environment, then women may still feel motivation to pursue short-term mating but experience dissatisfaction with the consequences. Studies show that women are more likely to regret having had sex with someone, compared to men who are more likely to regret having missed sexual opportunities, and women are more likely than men to experience negative emotions after engaging in "hooking up" (Lambert et al., 2003; Galperin et al., 2013). We hypothesize that at least some of women's regrets and negative experiences with short-term mating may come from environmental mismatch that results in them being less likely to gain the expected benefits from casual sexual encounters than they would have been likely to gain ancestrally.

Relocatable

Humans, as primates, have occupied large territories and home ranges and pursued a generally nomadic lifestyle, ranging from brief seasonal relocations to nearly continuous movement across the landscape throughout our evolutionary history. Data from modern foraging populations suggest that territory sizes range from small territories of less than 300 square miles in environments with dense and reliable resources, to greatly expanded territories that can stretch as far as 1,500 square miles in desert environments (Cashdan et al., 1983). These territory sizes mark the outer limits of a group's normal movements, primarily on foot, throughout the year. Marlowe (2005) has suggested that even relatively small home ranges in rich environments during the Late Pleistocene were probably on the order of about 110 square miles, far larger than those occupied by other primate species (by comparison, the largest territory occupied by extant chimpanzees is on the order of only about 13 square miles; Herbinger et al., 2001). However, these ranges are trivial compared to the distances that STRANGELY WEIRD people can travel with far less effort and risk. Modern transportation allows us to travel thousands of miles in hours, crossing mountains, continents, and oceans with ease. Geographic mobility in ancestral populations would not have provided even a fraction of the potential social opportunities represented by this level of mobility. In addition, the size of a foraging population's territory is generally negatively correlated with population density (Cashdan et al., 1983), so even those covering very large geographic territories have far more limited social novelty than in dense modern environments. The experience of complete social relocation, moving alone or with only one's immediate kin, to a large, anonymous, and entirely new community with few or no existing social bonds, would likely have been a rare event in such populations.

Such relocatability may alter perceptions of the costs and benefits of engaging in a number of mating-related behaviors, thus affecting a number of different mating-related adaptations. Behaviors that deviate from social norms, provoke retaliation, or have negative reputational consequences may be less costly if one can easily relocate. Mate poaching, the process of attempting to attract a romantic partner away from their current mate, provides an example of a mating-related behavior that can provoke retaliation and negatively affect reputation. Schmitt (2004) demonstrated that mate poaching was more common in world regions with more resources and more common in individuals higher in socioeconomic status. Although Schmitt argued that this was evidence that in less resource-rich environments, fidelity and biparental care are more important, an alternative explanation is that people with greater resources can more easily relocate and escape the negative consequences of poaching or being poached, increasing the frequency of this as a mating strategy.

Adaptations related to sexual exploitation provide another example in which the perception of unprecedented ability to relocate may have important implications. Are both men's and women's mechanisms related to sexual exploitation responsive to cues of extreme relocatability present in our current environment? One possibility is that men's mechanisms that motivate sexually exploitative behavior produce behavior flexibility in response to their ability to relocate. Unprecedented relocatability could then produce a corresponding increase in sexually exploitative behavior in men, indicating these psychological mechanisms are sensitive to the extreme range of this cue that exists in our modern environment. Even if men's psychological mechanisms are responsive to modern relocatability, women's mechanisms to protect themselves from sexual exploitation may not be sensitive to modern relocatability if ancestral relocatability was not correlated with women's on average greater ability to protect themselves from sexual exploitation. Another hypothesis is that neither men nor women are sensitive to the degree of modern relocatability because it did not exist ancestrally. If so, sexually exploitative behavior in men exposed to modern relocatability cues may not differ compared to men existing in an environment where cues to relocatability are similar to ancestral cue levels. Alternatively, both men and women's mechanisms may respond in ancestrally fitness-beneficial ways to cues to relocatability, despite the fact that this cue exists at greater intensity than ever before. Studies of women's fear of sexual assault do support the hypothesis that women's fear adaptations are sensitive to cues related to having relocated. Ferraro (1996) found that housing tenure (the length of time a woman had lived in her current residence) was negatively associated with fear of rape in women ages 18–34. Younger women who have more recently moved may be geographically isolated from family and social networks that ancestrally would have provided protection from sexual assault. Modern female university students may experience the extreme, mismatched version of having relocated if they have traveled hundreds of miles away to attend a university. We hypothesize that university women's fear of sexual assault may be stronger because of the extreme lack of cues of local protective family and kin. Relocating may have an even greater impact in the modern environment because of the extreme distances women may move.

Autonomous

People in our samples are often characterized by substantial autonomy in their mating decisions, a feature that is much less common in extant small-scale societies (Apostolou, 2007). Although ancestral human groups were likely characterized by a much lower average coefficient of relatedness than other primate groups, due to bisexual philopatry and dispersal, estimates from modern forager populations indicate that a child is likely to be related to approximately 50% of the adults in a band, at the level of 2nd cousins to her parents, with an additional 25% of the adults in the band being more distantly related (Hill et al., 2011). As adolescents, the stage in life when most individuals will begin to make mate choices, a person would be surrounded by aunts, uncles, grandparents, siblings, cousins, and in-laws. In contrast, many of the STRANGELY WEIRD people we study lack immediate contact with any kin at all, and live in a population of thousands or tens of thousands of unrelated, single, young people similarly unencumbered by closely watching kin.

There is evidence that kin, and parents in particular, have evolved psychology designed to influence offspring mate choice and have historically exercised, or attempted to exercise, that influence (e.g., Apostolou, 2012). Researchers have demonstrated that parents have preferences for who their child selects as a partner, and that these preferences sometimes differ from their child's preferences. Parents tend to emphasize a potential in-law's social and economic resources that can benefit the family group, while offspring emphasize the individual benefits that a potential mate can bring to the reproductive bond, in particular, genetic quality (e.g., Buunk et al., 2008; Perilloux et al., 2011; van den Berg et al., 2013). Arranged marriage is the norm across many small-scale subsistence populations. Even in groups in which arranged marriage is not practiced, parents are likely to have a great deal of influence as girls are almost universally married before they are 18 (Murdock et al., 2008). Although there is evidence that parental control in small-scale populations tends to weaken with age, the attempt at parental control would likely have been a consistent feature, particularly for young women entering a mating market and embarking on their first marriage.

Thus, many of the people we study now are exercising unprecedented autonomy in their mate selection. Candidate adaptations that are important to consider with respect to unprecedented autonomy include mate selection and relationship satisfaction adaptations. STRANGELY WEIRD people may make mating decisions, including who they select as a long-term mate, that do not reflect ancestral adaptiveness because the adaptations motivating these decisions lack sufficient input from parents and kin, who ancestrally would have exerted influence. Another possibility is that lack of input promotes indecision, or delays in long-term pair-bonding in people we study whose mechanisms evolved to incorporate parental assessment or approval as input. Census data tracking age of first marriage in the United States supports this hypothesis. Contrasted with the typical age of marriage cited above in modern small-scale societies, the median age of first marriage in the United States has increased over time and is at an all-time high of 29.8 years for men and 27.8 years for women (U.S. Census Bureau, 2018). Such delays may have downstream effects, including individuals having fewer offspring or being less likely to ever marry. Alternatively, reduced parental and kin influence could result in greater mate or relationship satisfaction in STRANGELY WEIRD samples because mate choice is a product of individuals' preferences alone, without having to compromise on their desires to satisfy family members.

Nulliparous

Nulliparous women and childless men are not an evolutionary novelty. However, the circumstances under which people are childless in our modern environment differs from ancestral childlessness. Based on data from modern foraging societies, ancestral women were likely to have had their first child by about age 19 (Robson et al., 2006), and most sexually active couples would have conceived eventually (Bailey and Aunger, 1995). We can compare this to current birth statistics- in the United States alone, the average maternal age at first birth steadily increased from 24.9 in 2000 to 26.3 in 2016 (Centers for Disease Control and Prevention, 2016). Ancestral nulliparity would have indicated that a woman either was not sexually active, or if she was, would indicate infertility, either with her, her partner, or the combination of the two of them (for a discussion of causes of childlessness reported in the ethnographic literature, see Betzig, 1989). Modern nulliparity, and childlessness in men, is often a conscious choice in our mismatched environment where some people precisely plan when and how to procreate.

One intuitive hypothesis about nulliparity or childlessness is that we would expect childless couples to be lower in relationship satisfaction. Relationship satisfaction is hypothesized to be an internal regulatory variable that tracks the fitness costs and benefits of remaining in or leaving a long-term relationship and functionally motivates relationship maintenance or dissolution behavior (Conroy-Beam et al., 2015). It is reasonable to hypothesize that whether or not a union had produced children could have evolved to be one input into relationship evaluation adaptations. Modern infertility statistics indicate that about 9% of men and 11% of women of reproductive age have experienced fertility problems, and similar rates ancestrally could have provided selection pressure to shape adaptations to motivate leaving a relationship when the couple was infertile (Chandra et al., 2013). However, studies of relationship and marital satisfaction in modern people do not support this hypothesis. One meta-analysis of studies of marital satisfaction found that parents report lower satisfaction than non-parents (Twenge et al., 2003). Additionally, studies that focus specifically on couples who explicitly desire children but are experiencing infertility have been inconclusive. Some demonstrate decreases in women's marital satisfaction associated with infertility, but others have demonstrated better marital functioning among infertile couples compared to fertile couples (Luk and Loke, 2015). One study even found that infertile couples experienced greater feelings of commitment and loyalty and emotional intimacy (Drosdzol and Skrzypulec, 2009).

These findings demonstrate that to test hypotheses about how nulliparity or childlessness will influence mating adaptations, their modern properties must be considered. Childless adults may be able to devote more of their energy and resources toward other pursuits- acquiring more resources, expanding social networks, increasing their status- that parents cannot because of the burdens of childcare (Shenk et al., 2016). This may demonstrate another instance of mismatch, where ancestrally more children would have been associated with increases in resource acquisition ability, expanded social networks, and increases in status (Crittenden, 2009; Wiessner, 2009). To the extent that their partnership improves their ability to pursue these alternative goals, nulliparous women and childless men may experience increases in relationship satisfaction that outweigh any negative effects of childlessness. The cue of a relationship having not produced a child may provide only one piece of input into mating adaptations, therefore; testing whether or not it is a cue requires controlling for other possible inputs that may mask its effects.

Interestingly, there is evidence that cross-culturally, infertility does often lead to divorce (Betzig, 1989). There are two possibilities for explaining why recent data about infertility and relationship satisfaction does not fit with historical data about infertility and divorce. Recent studies about relationship satisfaction could represent a change in how people in Western societies perceive childlessness. Not having children may be less of a cause for relationship dissolution than it was before, another way in which people we study may be mismatched. Alternatively, once a couple has children, divorce may be less desirable because of the potentially negative effects it could have on offspring, motivating couples to stay together even if they are less satisfied with one another. Thus, interpreting these findings, and what they mean for the underlying design of psychological mechanisms that motivate relationship dissolution, requires thinking about the mismatched elements of the people studied.

Whether or not a person already had children, and the degree of parental investment existing children required to survive and to gain competitive advantage in their sociocultural context, could have altered the fitness consequences of mating decisions, and mating mechanisms may have evolved to be calibrated by the presence and status of existing offspring (Goetz, 2016). Because women ancestrally had the greater obligatory parental investment (Trivers, 1972), we should expect parenting status to particularly impact women's psychology. For example, mothers faced the adaptive problem of obtaining a mate who did not pose a threat to her existing children- a problem not faced by nulliparous women (Daly and Wilson, 1985). Children may also influence mating cognition indirectly through their effect on parents' mate value, and women's mate value in particular. Men in the United States report being less willing than women to marry someone with a child, and in the Kipsigi in Kenya, grooms' families offer a lower bride-price for women who already have a child by another man (Borgerhoff Mulder, 1988; Goldscheider and Kaufman, 2006). This combined evidence suggests that having children negatively impacts women's mate value, likely more than men's mate value. Mate value has been hypothesized to influence a variety of adaptations, including mate preference mechanisms and those regulating and relationship maintenance behavior (Buss and Shackelford, 2008; Edlund and Sagarin, 2010; Starratt and Shackelford, 2012). Studying these nuances in the design of mating adaptations requires samples that vary in offspring number. Additionally, prior to contraception, the majority of a person's mating career would have occurred when they were already parents. Therefore, studies of that include only nulliparous women and childless men may only capture a narrow slice of the design of mating adaptations.

Group Segmentation

Ancestral bands were limited to about 150 adults who regularly interacted with one another, and who were likely to be related in some way either by blood or marriage. Not only did everyone know each other, but they intimately understood each other's lives- the challenges, the labors, the entertainments, the daily, seasonal, and annual routines, and the random natural or social events that interrupted those routines- because they shared them (Kelly, 1995). Additionally, although there were divisions of labor by age and sex and variations in skill and specialization, everyone had some familiarity with many of the skills and tasks necessary for survival, including tool-making, food production, and caregiving. One of the consequences of such interconnectedness is that there is a high degree of consensus in small-scale populations regarding the relative social status and the particular strengths and weaknesses of others in the community: who is the best hunter, who is the best mother, who has the best garden, who is the strongest fighter, who is the worst liar, who is the biggest cheater (Bird et al., 2001; Gurven and von Rueden, 2006; Pillsworth, 2008; Escasa et al., 2010). In addition, there is strong consensus about the value of these various traits, including which traits matter most in a reproductive partner. In a Shuar community, for example, there was almost 100% consensus among men that whether a woman makes good chicha (manioc beer) is more important than if she was a virgin before marriage (Pillsworth, 2008). Even if specific community assessments are not very accurate (for example, hunting reputation among the Hadza does not appear to be a particularly good predictor of actual hunting returns, Stibbard-Hawkes et al., 2018), the reproductive consequences of one's reputation are important, and likely reflect mating-relevant underlying qualities (Apicella et al., 2007; Apicella, 2014; Smith et al., 2017).

However, in STRANGELY WEIRD contexts, people are members of numerous, non-overlapping, sometimes highly specialized, social groups that we may shift rapidly between. In a 12-h period, a STRANGELY WEIRD person can go from a new job where they are the lowest in status and influence, to a game with their long-standing recreational softball team where they are the lead hitter, to post-match drinks at a bar among strangers. A person's reputation and standing among one social group may not be known to those outside that group. Additionally, characteristics that result in status gains or desirability among one group may not have the same influence among a different group. Although many of the characteristics that are desired in mates- physical attractiveness, kindness, intelligence- are likely perceptible across contexts, certain traits might be expressed more within one group compared to another, and one's relative standing on each trait could shift from group to group.

The potential consequences of this mismatch are important for researchers studying adaptations that function to track relative social valuation, mate value, and desirability of the self and others. A person's mate value depends on their relative standing on the multitude of traits that people assess when selecting a mate (Conroy-Beam et al., 2016). Modern social group segmentation allows us to test hypotheses about the extent to which our self-perceived mate value updates when we rapidly shift from one social group to another. Furthermore, there is evidence that the diversity of social roles available to STRANGELY WEIRD people facilitates specialization and differentiation in personality (Lukaszewski et al., 2017), opening up new dimensions of mate evaluation. The existence of multiple groups likely has different consequences for men and women. Because physical attractiveness is a more important component of women's mate value compared to men, for example, women's mate value should change less from group to group compared to that of men (e.g., shifting from a coed campus study group to a coed softball game).

Additionally, social group segmentation may make it easier for people to shield undesirable or negative information about themselves from potential mates because their behavior and attitudes expressed in one group are unknown to those in a different group. Both men and women engage in deceptive tactics to attract mates that involve exaggerating their desirable qualities and masking their undesirable qualities (e.g., Tooke and Camire, 1991). The mismatched characteristic of extreme group segmentation allows us to test the extent to which adaptations motivating deception are sensitive to this mismatched context in which deception may be more effective, and we can test if there are increases in deception in mating when people's social groups are more segmented. Similarly, extreme group segmentation provides researchers the opportunity to study the design of deception-detection adaptations in contexts where information about others may be more limited than it would have been ancestrally. One possibility is that because deception-detecting adaptations did not evolve in an environment in which social groups were so segmented, they fail to detect deception as well in contexts where a person's interactions with the deceiver are limited to a particular isolated social group.

Educational Setting

University student samples likely deviate from both non-university samples and ancestral populations in important ways. Students are surrounded by many mate options, as well as many mating competitors, who are similar in age and socioeconomic status to themselves. Although university students are often legally classified as adults and may live apart from their families, many of them remain financially and emotionally reliant on their parents. Additionally, many universities are now female-biased at the undergraduate level, and operational sex ratio is related to human mating patterns (e.g., Schmitt, 2005; Stone et al., 2007; Kruger and Schlemmer, 2009). A surplus of women in the mating pool, for example, tends to shift mating behavior more toward short-term mating, such as "hookups" and "friends with benefits" (Buss, 2016). Each of these features of university students may be important to consider from the perspective of mismatch and are cases where input may be of a level of intensity outside the range ancestral humans ever encountered.

Researchers should consider how students in their studies are interpreting questions asked of them in a research setting, and how their behavior may be shaped by their context. Li et al. (2013) argued that previous research using speed-dating methods and university samples may have not replicated sex differences in mate selection because those study designs lacked mate options who represented low-end variation on key traits like financial prospects and physical attractiveness. In one of their studies, they demonstrated that a relatively low status college student was rated as low in earning prospects when participants evaluated this person among a group of other college students. However, when the same person was evaluated among a group that contained low status individuals from the general population (e.g., a non-college graduate working at a mall), the low status college student was rated as having average earning prospects. Across three studies, Li et al. (2013) demonstrated that sex differences in mate preferences are reflected in mate selection in university students when the study design includes the full range of variation on sex-differentiated preference dimensions. These studies demonstrate that when we study college students, the reference group they are using to make comparisons matter. Outcomes will differ if they are restricting their evaluations to other university students, compared to if they are considering the population as a whole. They also reveal the importance of considering the mismatch of the people and contexts studied. Li et al. (2013) criticized the design and data interpretations of previous studies precisely because those studies did not take into account the evolutionary mismatch of the university students and setting.

Lots of Options

STRANGELY WEIRD people have potentially endless options for sexual and romantic partners. Ancestrally, humans lived in small groups, with average band sizes estimated to not surpass a maximum of about 300 total people, including children under the age of 15, who typically make up nearly 50% of a forager group (Jones et al., 1992; Marlowe, 2005). Such bands might occasionally come together into much larger tribal units of more than 2,000 individuals, but several lines of evidence suggest that humans cognitively track only about 150 individuals (Dunbar, 1993; Hill and Dunbar, 2003). The pool of potential mates was even further limited to currently available reproductive-age adults of the preferred sex. Many of the people we study live in unprecedentedly massive metropolitan areas, where even "small" cities can contain more inhabitants than our ancestors would have met in a lifetime. Our research participants are constantly exposed to novel people, and have access to a large, people-dense, geographic radius of accessible mates.

Researchers have demonstrated that mating behavior and cognition differ depending on the number of potential partners being evaluated. Lenton and Francesconi (2010) compared "small" speed dating events, where participants met with 15–23 potential partners to "large" speed dating events (24–31 potential partners). They found that visible cues, like height and weight had a stronger influence on mate choice at large events, while non-visible cues, like occupational status and education had a larger influence at small events. Experimental research in which female participants evaluated four, 24, or 64 mate options has demonstrated that women report using different heuristics depending on option number. Women selecting one profile from four were more likely to report using a weighted average strategy where they evaluated trade-offs across attributes within a profile. Women evaluating larger sets were more likely to use an elimination-by-aspects strategy, where they eliminated options by evaluating across profiles one attribute at a time (Lenton and Stewart, 2008). Other research has addressed satisfaction with mate choice decisions when there are numerous options. D'Angelo and Toma (2017) found that online daters who chose from 24 options were less satisfied with their choice compared to those who chose from six options. Furthermore, those who chose from the larger set *and* were given the option of reversing their decision 1 week later were the least satisfied. In general, these studies demonstrate that when participants are making mating decisions in contexts in which they have many options, they think and behave differently. When options are more limited people: (1) do assess the non-visible characteristics that typically come up in studies of mate preferences, (2) rely on heuristics that involve assessing potential partners holistically across a variety of attributes, and (3) are more satisfied with their mating decisions and less subject to "choice overload" effects (Iyengar and Lepper, 2000). These findings support the hypothesis that our adaptations are sensitive to variation in the number of available partners.

However, the number of options available to many people we study represents an input into mating mechanisms that is several orders of magnitude more intense than ancestral humans were likely to have experienced. An open question is how this supernormal stimulus interacts with our mating adaptations. Do these adaptations simply ramp up their outputs in response to the novel stimulus? Or are other decision-making mechanisms co-opted in our modern environment to sort through our options in ways that would not have occurred ancestrally? Alternatively, because our mating mechanisms were shaped in environments with so many fewer options, are there limits to how responsive we should expect mating behavior to be to this unprecedented option number? Even if there are endless options, perhaps people do not *perceive* their world as though there are – and, worse for them, they may use decision strategies better suited to a bygone past, rather than strategies that are tailored to the decision problem they are actually facing.

Young

Youth is not an evolutionary novelty; however, Western young adults differ in many ways from ancestral people in their late teens-20s. Data from hunter-gather groups indicate that children begin hunting and gathering in early childhood and are contributing substantially to a family's caloric needs in adolescence, compared to modern children and adolescents who often do not contribute at all to family livelihood, or only minimally (Hawley, 2011; Crittenden et al., 2013; Konner, 2017). Menarche in women in hunter-gather groups occurs in the late-teens, compared 11–12 years of age in modern, Western girls (Konner, 2017). Sexual behavior is typical in adolescent hunter-gatherers, and adults exert only weak control over adolescent sexuality (Konner, 2017). Additionally, STRANGELY WEIRD children are often segregated by age, limiting interactions, socialization, and learning from older and younger individuals (Hawley, 2011). Overall, by the age of 18, ancestral individuals likely already developed adult skills related to subsistence, interacted with group members across all ages, developed some reputation and social standing, engaged in sexual behavior, if female were likely married, and may already have had children.

In contrast, modern Western young adults are just learning the ropes of self-sufficiency, many are experiencing their first sexual relationships, they often are not parents, and are in a novel extended period of skills and career building. The behavior we observe in STRANGELY WEIRD young adults may more accurately reflect mating behavior in ancestral adolescents rather than their same-age counterparts. The mismatch in age of menarche is particularly interesting. Ancestrally, sexual exploration in adolescence would have been less costly to pre-menarchal girls. The potential costs are higher in modern Western girls, who on average have fewer years of cognitive and social development to guide their decision-making prior to the onset of reproductive capability (Coe and Steadman, 1995).

Evolutionary thinking does provide a foundation for making subtle, sex-differentiated, predictions about how age should relate to mating cognition and behavior. For example, women's reproductive window is limited compared to men's and their probability of conceiving peaks when they are in their mid-twenties and tapers off until menopause. One of the starkest sex differences in adaptive problems would have occurred when men and women were in their mid-40s through 50s, when women experienced menopause. The Grandmother Hypothesis suggests that menopause was adaptive in women because they would have experienced greater fitness gains from investing in current offspring and current or future grand-offspring than by continuing to reproduce (Hawkes et al., 1998). Ancestral men would have experienced almost the opposite selection pressure- their status and resource holdings could accrue with age, providing them with more mating opportunities. Among the Tiwi of northern Australia, for example, men under age 30 rarely have enough status to attract a wife (Pilling and Hart, 1960). Young people are, and ancestrally were not, the only people engaged in mating-related behavior and decision-making. Studies that focus exclusively on young adults limit our ability to test age-dependent design features of adaptations. And there is a danger in testing and retesting hypotheses about universal design on a homogenous subgroup of individuals because doing so provides a narrow slice of information and may not reflect the range in variation in human mating behavior across the lifespan predictable from evolutionary theory.

DISCUSSION

Although each mismatched characteristic requires unique analysis, there were commonalities in our approach across characteristics. Existing ethnographic research, and research from anthropologists, behavioral ecologists, biologists, and psychologists has developed our understanding of the features of humans' ancestral past. We drew on this interdisciplinary research to develop an understanding of how each particular characteristic embodied evolutionary mismatch. We then considered how an environment mismatched on a particular characteristic would influence functioning of specific mating-related adaptations. Fully understanding mismatch requires both a keen understanding of ancestral conditions and an appreciation of the design of information-processing mechanisms that regulate behavior. This process led to novel hypotheses that a researcher could investigate that would address human mating adaptations through the study of STRANGELY WEIRD people.

We focused on STRANGELY WEIRD people; however, even non-WEIRD people are mismatched from ancestral conditions-many now have access to smart phones, buses and other forms of transportation, and can purchase food and supplies. The approach outlined in this paper should not be limited to the study of university undergraduates, but it important regardless of the particular population being studied. Additionally, we focused our analysis on the domain of human mating, but much of what we have argued here can and should be applied to research in other areas of human psychology and behavior as well, such as cooperation, coalitions, status hierarchies, and kinship. Even the characteristics we identified may also be important to consider for those studying other types of social relationships, interactions, and perceptions.

Organizing and Expanding on Mismatched Characteristics

We focused on just nine mismatch characteristics, but these represent just a small fraction of the many potentially important ways in which modern environments differ from the ancestral environments that forged our mating psychology. Another important mismatch not considered in detail, for example, is the absence of small-group warfare that characterized small-group living throughout much of human evolutionary history (e.g., Ghiglieri, 1999). Such warfare would have had profound effects on mating. These include mate acquisition through offensive raids and higher male than female mortality, in turn creating a sex-ratio imbalance of a surplus of women. This imbalance, in turn, may have created conditions fostering polygyny. In short, the absence of small-group raids and war in the modern environment renders it highly discrepant from ancestral environments – one of many additional mismatches affecting human mating that we have not considered in detail.

These nine mismatch characteristics can also be arrayed on higher order dimensions of mismatch, which may facilitate identifying other important mismatch characteristics. Li et al. (2018) have provided a starting point for considering the broader dimensions of mismatch. They generated four dimensions along which mismatch phenomena can be arrayed: source, type, consequences, and causes. *Sources* can be natural or human-generated. They argue for two *types* of mismatch- "forced" occurs when a new environment is imposed on an organism and "hijacked" are when novel stimuli are favored by mechanisms over stimuli that would have existed ancestrally, to which the mechanism originally evolved in response. The *consequences* dimensions involves defining mismatch phenomena on their mismatched consequences for an organisms' fitness and/or well-being and values compared to ancestral environments. Finally, they argued that the *causes* of mismatch are either changes in input into a psychological mechanism (input may be more or less intense than it was ancestrally, entirely missing in the modern environment, or novel cues may mimic ancestral cues), or changes to the consequences of the output of an adaptation.

Many of the STRANGELY characteristics can fit easily into their dimensional framework. For instance, Relocatable, Autonomous, Group segmentation, Educational setting, and Lots of options are extremes on the causes dimension in that they represent unprecedented intensity of input to which individuals are exposed. Social media provides novel cues that may mimic ancestral cues. We also offer another dimension of mismatch phenomena to consider- mismatch between the modern properties of particular characteristic and the ancestral properties of that characteristic. Temporary relationships, Nulliparous, and Young are characteristics that require this type of consideration. Organizing along other dimensions may be more useful in other circumstances. For example, researchers specifically focused on the implications of mismatch on individual well-being may place greater focus on the consequences dimension and a helpful reviewer of this paper suggested other dimensions of mismatch. One dimension suggested by the reviewer was a "similar-different in information conveyed by a cue" dimension. The advent of cosmetic surgery, for example, may result in facial wrinkles providing less information about an individuals' age (and, perhaps, more information about their resources) than facial smoothness would have provided ancestrally. No single dimensional framework is likely to offer optimal resolution for clearly identifying all mismatch characteristics that are relevant for a particular research question. Preferred dimensions or types may depend on the researcher's goals and this dimensional space should evolve over time as researchers continue to test mismatch hypotheses.

Mismatch and the Variability of Human Behavior

Research on human mating from an evolutionary perspective has demonstrated how evolved psychology produces behavioral flexibility and variability. Not all observed characteristics unique to the people we study require mismatch framing. Many modern, culturally specific behaviors and products of our behavior can be understood as instances of evoked culture, and behavioral flexibility and cultural differences are expected to occur as functional output of evolved psychological mechanisms (Tooby and Cosmides, 1992). However, these processes also contribute to generating environmental mismatch. Our evolved psychology has produced social media and devices on which to consume it, fostered the development of large, anonymous societies, and created medical technologies that allow us to precisely plan when we will reproduce. But understanding how these novel features of people and environments interact with our adaptations requires careful consideration. Their influences on both the people studied and the researchers studying them should be examined.

Some characteristics generated open questions about adaptation design that only become testable *because* of sample mismatch. For example, any adaptation that tracks option number evolved in an environment where people were exposed to fewer options than they are now. The benefits of studying samples mismatched on this characteristic is that we can determine if adaptations respond differently when option number varies outside a range that would have existed ancestrally- or if they do not. In this way, mismatch is not a barrier that prevents us from being able to establish evidence of universal psychological design. Instead, mismatch can be a useful tool.

Using a mismatch perspective also reminds researchers that the output of adaptations observed in modern people may seem curiously "maladaptive" if we attempt to assess the output's current fitness costs and benefits. Outside the mating domain, our evolved food preferences adaptations provide a simple example. In an ancestral environment of greater food scarcity without refrigeration and grocery stores, motivation to opportunistically consume high-calorie foods would have been functional. The design features of our food preference adaptations, shaped by that environment of potential scarcity, now motivate many of us to eat far more than is necessary in our mismatched, food-rich environment, to the detriment of our health and longevity. We expect that the output of mating adaptions in our mismatched modern environment may produce similar outcomes. Consider relationship satisfaction, an adaptation hypothesized to be sensitive to the presence and number of potential high-quality alternative mates (Conroy-Beam et al., 2016). Ancestrally, lower relationship satisfaction in response to better options, possibly motivating leaving a current mate, may have been adaptive. However, in our modern environment of perceived abundance of high-quality mate options, such an adaptation could produce never-ending relationship dissatisfaction and difficulty maintaining pair-bonds. This is part of why focusing on current adaptiveness of behavior is inappropriate to understand the underlying design of our psychology (Tooby and Cosmides, 1990; Confer et al., 2010). Researchers interested in the mating behavior that results in distress, negative emotions, and seemingly dysfunctional outcomes may be able to better understand those phenomena by employing mismatch concepts.

Some of the adaptations and mating behavior we discussed relate to the darker sides of human mating- including mate poaching, sexual conflict, and rape. Our analysis sheds light on particular features of our modern environment, such as relocatability and anonymity, that we predict could increase such phenomena. Researchers interested in designing interventions to reduce these societal ills can benefit from thinking about mismatch and how evolved mechanisms respond to cue levels present in our modern environment.

Recommendations and Conclusions

Mismatch thinking is complicated. So are the potential implications of evolutionary mismatch. Although we discussed each mismatch characteristic separately in this paper, any researcher employing mismatch concepts will practically find themselves evaluating and framing research questions with respect to multiple characteristics. Case in point, we described and hypothesized about incels in the subsection on temporary relationships, but that discussion also would have been appropriate when discussing social media. Many psychological and behavioral phenomena of interest should be considered with respect to multiple mismatched features simultaneously-which may lead to competing hypotheses. For example, we hypothesized that modern relocatability may increase sexual conflict, but the absence of small-group warfare in STRANGELY WEIRD people could have the opposite effect on sexual conflict. We even posed competing hypotheses generated by considering a single characteristic- autonomy in mate choice may decrease relationship satisfaction if influence from kin increases satisfaction, but mate choice autonomy could increase satisfaction if it is associated with less compromising of preferences. No single study is expected to capture the full complexity of any adaptation, or test all relevant mismatch hypotheses. But we are optimistic that the growing body of researchers who use an evolutionary perspective to study human mating will achieve great strides in unraveling the complicated nature of mating adaptations by engaging in the complicated endeavor of mismatch thinking.

We provide four general recommendations to facilitate the development of research programs that address mismatch. These recommendations are intended to build on the high-quality work that has been conducted on human mating from an evolutionary perspective. Researchers have made great strides in explaining the underlying universal design of mating-related adaptations, including those related to mate preferences, romantic and sexual jealousy, incest avoidance, and mating strategies (e.g., Schmitt, 2005; Lieberman et al., 2007; Buss, 2018; Buss and Schmitt, 2019). The arguments presented here do not discount existing research. We acknowledge that much of this research has been conducted in accordance with our recommendations. We offer these insights as a model for researchers going forward with the hope that a more explicit focus on mismatch will be one of the tools researchers of human mating can use to better develop and refine their work.

First, we suggest incorporating mismatch concepts into existing best-practices on how to conduct research using an evolutionary perspective. As evolutionary psychology and related fields have developed over time, researchers have elucidated how to conduct research from an evolutionary perspective. They have addressed all stages of the research process, from hypothesis generation, to study design, to data interpretation (e.g., Barkow et al., 1992; Lewis et al., 2017). Adding consideration of mismatch of the intended study subjects, particularly at the study design and data interpretation stages, should become standard practice. Researchers should consider their own mismatch throughout the process to identify instances where their own mismatched circumstances may bias their thinking.

Second, we identified nine characteristics that we believe are particularly important to consider in the field of mating behavior and psychology. These are intended to provide a starting point, but not an exhaustive list, for elements of mismatch to consider. We hope others will expand and refine this list (e.g., small-group warfare as another good candidate). Certain characteristics may be more important than others to address depending on the specific mating-related adaptations being studied.

Third, we will improve our research by proposing and testing hypotheses explicitly about mismatch when possible. Cross-cultural research, and comparisons with small-scale societies are ideal in some cases, but even within Western societies it may be possible to examine populations that vary on the identified mismatched characteristics. If it is not possible to specifically incorporate mismatch into study hypotheses or design, researchers should include these ideas in the discussion of their results. This will improve our science over time and pave the way for future research that may be better able to address mismatch.

Fourth, we suggest highlighting when a mismatched sample may actually be beneficial for testing a particular hypothesis. Characteristics that generate unprecedented levels of input into mechanisms, or result in the absence of input, are necessary to assess the range of input to which mechanisms are responsive. Effortfully addressing the benefits of a particular sample also should assist researchers in employing appropriate caution in interpreting what data from that sample does tell us about the universal design features of psychological adaptations.

To conclude, we advocate for the explicit consideration of sample and researcher mismatch throughout the research process when studying mating-related adaptations and anticipate that this will propel progress in our understanding of human nature.

AUTHOR CONTRIBUTIONS

CG developed and conceived the central ideas, structure of the manuscript, and had principle writing responsibility. EP and DC-B contributed to the original concept and writing. DB provided substantive feedback and revisions on all sections of the manuscript. All authors contributed to the manuscript revision, read, and approved the submitted version.

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Life History and Multi-Partner Mating: A Novel Explanation for Moral Stigma Against Consensual Non-monogamy

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Life history theory (LHT) predicts that individuals vary in their sexual, reproductive, parental, familial, and social behavior according to the physical and social challenges imposed upon them throughout development. LHT provides a framework for understanding why non-monogamy may be the target of significant moral condemnation: individuals who habitually form multiple romantic or sexual partnerships may pursue riskier, more competitive interpersonal strategies that strain social cooperation. We compared several indices of life history (i.e., the Mini-K, the High-K Strategy Scale, pubertal timing, sociosexuality, disease avoidance, and risk-taking) between individuals practicing monogamous and consensually non-monogamous (CNM) romantic relationships. Across several measures, CNM individuals reported a faster life history strategy than monogamous individuals, and women in CNM relationships reported earlier pubertal development. CNM individuals also reported more social and ethical risk-taking, less aversion to germs, and greater interest in short-term mating (and less interest in long-term mating) than monogamous individuals. From these data, we discuss a model to explain how moral stigma toward non-monogamy evolved and how these attitudes may be mismatched to the modern environment. Specifically, we argue that the culture of sexual ethics that pervades contemporary CNM communities (e.g., polyamory, swinging) may attenuate risky interpersonal behaviors (e.g., violent intrasexual competition, retributive jealousy, partner/child abandonment, disease transmission) that are relatively more common among those who pursue multi-partner mating.

Keywords: life history, consensual non-monogamy, morality, sociosexuality, risk-taking, disease avoidance

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INTRODUCTION

Consensual non-monogamy (CNM) refers to any romantic relationship wherein people form consensually non-exclusive romantic or sexual partnerships. Those who practice CNM tend to experience greater moral stigma than those within exclusively monogamous romantic relationships. Compared to monogamous individuals, people are more likely to hold negative attitudes and beliefs about (Conley et al., 2013a; Moors et al., 2013; Grunt-Mejer and Campbell, 2016; Burleigh et al., 2017; Thompson et al., 2018), dehumanize (Rodrigues et al., 2018), and socially distance themselves from Balzarini et al. (2018a) individuals within CNM relationships. Compared to CNM relationships, monogamy is presumed to improve sexual frequency and desire, sexual health, relationship satisfaction, experiences of jealousy, and childcare practices (Conley et al., 2013a,c,d) and is widely believed to be morally superior to CNM (Conley et al., 2013a; Matsick et al., 2014; Grunt-Mejer and Campbell, 2016).

Importantly, these perceptions are discordant with actual practices and outcomes of CNM. For example, CNM individuals are presumed to have worse sexual health than monogamous individuals (Conley et al., 2013a) yet report similar or better sexual health practices compared to monogamous individuals (Conley et al., 2012, 2013b; Lehmiller, 2015). Individuals within CNM relationships report unique benefits from forming multiple intimate relationships (see Moors et al., 2017), including diversified need fulfillment (Mitchell et al., 2014; Muise et al., 2019), more frequent social opportunities (Moors et al., 2017), and more fluid sexual expression (Manley et al., 2015). These benefits are associated with relatively greater relationship satisfaction (Rubel and Bogaert, 2015; Levine et al., 2018), particularly when an individual's personality is matched to their relationship structure (e.g., when someone with a more unrestricted sociosexuality pursues CNM; Rodrigues et al., 2017, 2019). Therefore, it seems that either monogamy or CNM can improve social relations, romantic satisfaction, and mental health when the option to pursue diverse romantic and sexual strategies allows someone to find and fill their niche.

The harm that third-party stigmatization can introduce to the well-being of people in CNM relationships (e.g., Kirkman et al., 2015) highlights the need to explain moral stigma toward these relationship structures. Most current explanations relate stigma to CNM's defiance of monogamy as a predominant culture practice (i.e., mononormativity; see Emens, 2004). Day (2013) has argued that stigma against CNM is rooted in defense of a committed relationship ideology, which is the assumption that monogamous marriage is the only relationship structure that provides desirable social and relational outcomes, like loyalty, order, and quality childcare (see also Day et al., 2011). Similarly, many authors have adopted a complementary feminist lens which broadly argues that the predominance of monogamy is a sociohistorically enforced standard that has restricted women's and other social minorities' agency, sexual expression, capacity to form extended social support networks, and sexual health (Ziegler et al., 2014; Klesse, 2018; Moors, 2019). Collectively, these perspectives have inspired researchers to document and correct misinformation about CNM practices and outcomes with the hope of alleviating the harmful consequences of stigma.

Although identifying and critically evaluating stereotypes can be an effective intervention against prejudice (Hill and Augoustinos, 2001; Hogan and Mallott, 2005; Kulik and Roberson, 2008; Ateah et al., 2011; Hutzler et al., 2016), studying the evolved psychological mechanisms that underlie prejudicial beliefs against CNM may explain their persistence within cultures resistant to these interventions and help frame the underlying moral anxieties and errors in cognition that lead people to justify wrongful discrimination against CNM. Salvatore (2013) argues that identifying the source of stigma against CNM will require a careful understanding of how CNM is devalued relative to monogamy, either via a lack of familiarity with CNM and its outcomes, or via a perceived threat (i.e., that CNM introduces instability or harm to people and their communities). The current study explores the latter possibility that moral aversion stems from the perception that CNM is a threat to well-being. We propose a novel framework for understanding this stigma by assessing the association between CNM and life history strategies.

Life history theory (LHT) is a framework for understanding individual variation in sexual, reproductive, parental, familial, and social behaviors across the lifespan [reviewed in Figueredo et al. (2006); see also Del Giudice et al., 2015]. It predicts that organisms vary adaptively in how they allocate limited time and resources toward growth and reproduction. This variation can be meaningfully divided into two predominant strategies: a slow life history, whereby individuals delay sexual development and reproduction (i.e., invest more in relatively fewer offspring) and a fast life history, in which individuals experience earlier sexual maturity and produce a greater quantity of offspring (i.e., invest less in relatively more offspring). Each strategy prepares an organism to extract value from its environment according to the physical and social challenges that it experiences throughout development. In relatively more stable environments (e.g., high socioseconomic status, low mortality rate), delayed and restricted reproduction allows resources to be channeled into a few offspring likely to survive. In unpredictable environments, accelerated reproduction hedges the risk of investing too deeply into a single child when that investment is unlikely to pay off.

Although recent work criticizes the validity of applying LHT to trait variation within humans (e.g., Nettle and Frankenhuis, 2019; Zietsch and Sidari, 2019), this predictive lens has been useful for studying psychosocial developmental plasticity within underprivileged environments (see Kuzawa and Bragg, 2012). Relative to a slow life history strategy, people with faster life history strategies prefer immediate over delayed rewards (Griskevicius et al., 2011), reproduce earlier (Boothroyd et al., 2013; Hehman and Salmon, 2019), have more casual sex (Dunkel et al., 2015; Salmon et al., 2016), experience earlier sexual debut and report greater sexual risk-taking (James et al., 2012), pursue social status via dominance rather than prestige (Lukaszewski, 2015), score higher on measures of psychopathy (e.g., boldness, aggression, and disinhibition; Međedović, 2018) and dark personality (i.e., impulsivity, antisociality, entitlement/exploitativeness, Machiavellianism, and aggression; McDonald et al., 2012), and are more likely to use psychoactive substances (Richardson et al., 2014). These traits are advantageous in harsh, unpredictable environments to the extent that they help an individual to competitively capitalize on limited resources. That is, if the future is relatively unpredictable, investing effort into immediate rewards may be a more successful survival strategy than long-term investments that pay off more gradually (Pepper and Nettle, 2017; Ellis and Del Giudice, 2019).

To the extent that CNM relationships are promiscuous, multi-partner mating systems, people may assume that CNM individuals practice faster life history strategies relative to those in monogamous relationships. People who pursue a sociosexually unrestricted mating strategy are perceived to have faster life history qualities (i.e., high impulsivity, high aggression, less education, and origination from more desperate ecologies) and are rated as less trustworthy (Moon et al., 2018). These perceptions appear to be at least somewhat accurate. People from more deprived neighborhoods (i.e., a proxy of fast life history) are less generous in a Dictator Game (Nettle et al., 2011). Likewise, regions with high rates of polygyny and socioeconomic inequality have higher rates of male relative to female mortality (Kruger, 2010), suggesting that these communities experience more intense and violent competition between men for access to limited resources. Furthermore, people readily form lay beliefs about others' life histories, such that those described as originating from desperate ecologies (e.g., low socioeconomic status, high mortality rates, high crime rates) are presumed to have faster life history qualities (Williams et al., 2016). This suggests that people instinctively use sexual behavior to predict others' personal qualities (e.g., risk propensity, trustworthiness).

This intuition may explain patterns of moral disgust and condemnation of CNM. Individuals experience moral disgust when a social violation threatens to depose a moral rule that personally benefits them (see Tybur et al., 2013). For example, someone's preference for long-term mating (see Gangestad and Simpson, 2000) predicts their endorsement of moral rules that constrain others' sexual behaviors (Weeden et al., 2008; Kurzban et al., 2010). People then condemn others' behaviors to strategically rally public support for social policies that they perceive to be beneficial (DeScioli and Kurzban, 2009, 2013). People may condemn CNM because they believe that it enables fast life history behaviors (i.e., risk taking, interpersonal antagonism), and that endorsing it will destabilize social unity and cooperation. That is, those who wish to preserve stable, cohesive communities may condemn CNM insofar as sexual promiscuity is indicative of faster life history traits that produce intra-group conflict (e.g., aggressive competition over mates; partner retribution).

People may generally assume that individuals within CNM relationships possess faster life history traits, but it is currently unknown whether these perceptions are accurate. People in CNM relationships consistently report a more unrestricted sociosexuality (Morrison et al., 2013; Rodrigues et al., 2016, 2017, 2019; Mogilski et al., 2017, 2019; Balzarini et al., 2018b). However, it is possible that they do not possess other fast life history qualities that interfere with the long-term, cooperative values endorsed by slow life history strategists. Certainly, the defining quality of CNM relationships is that practitioners are expected to follow strict ethical guidelines that reduce sources of suffering common to multi-partner mating systems (e.g., jealous anxiety, STI transmission, competitive aggression, partner or child abandonment; Hardy and Easton, 2017). Because of the association between unrestricted sociosexual behavior and faster, riskier, competitive interpersonal behaviors, those who stigmatize these relationships may assume that unrestricted sociosexuality is a good predictor of immoral behavior and unethical decision-making.

This study assessed whether life history varies between individuals within monogamous and consensually non-monogamous romantic relationships. We examined life history variation among three groups: (1) those who are currently romantically involved exclusively with only one other person (i.e., monogamous), (2) those non-exclusively involved with only one other person (i.e., open relationship), and (3) those non-exclusively involved with more than one other person (i.e., multi-partner relationships). We measured life history using two self-report measures: the Mini-K (Figueredo et al., 2006) and the High-K Strategy Scale (HKSS; Giosan, 2006), and several complementary measures including self-reported pubertal development (Petersen et al., 1988), sociosexuality [i.e., the Multi-dimensional Model of Sociosexual Orientation (MMSO); Jackson and Kirkpatrick, 2007], the Domain-Specific Risk-Taking Scale (DOSPERT; Blais and Weber, 2006), and the Perceived Vulnerability To Disease Scale (PVDS; Duncan et al., 2009).

Overall, we predicted that individuals within monogamous relationships would report a slower life history than those within open and multi-partner CNM relationships. We expected aspects of life history that correspond to greater sexual promiscuity (e.g., unrestricted sociosexuality, earlier pubertal development) would be higher among open and CNM participants than among those in monogamous relationships. However, to the extent that those within CNM relationships follow popular guidelines that prevent interpersonal exploitation and dangerous sexual practices (Hardy and Easton, 2017), we predicted that they would not be more willing to exploit others for personal gain or to expose themselves to pathogens (e.g., STIs) than monogamous individuals. We expected risk-taking, and in particular facets of risk-taking that expose others to danger (i.e., ethical and health risk-taking) and perceived vulnerability to disease to be no different than those in monogamous relationships. Furthermore, we used the MMSO to measure sociosexuality because it measures interest in short- and long-term relationships on separate continua. Compared to the SOI-R, which has already been used extensively in prior CNM research, this will permit us to not only examine whether CNM individuals are more interested in casual sex than monogamous individuals, but also whether they are relatively less interested in long-term, committed relationships. Although the former has been well-documented (Morrison et al., 2013; Rodrigues et al., 2016, 2017, 2019; Mogilski et al., 2017, 2019; Balzarini et al., 2018b), the latter has not. A person could theoretically be high or low on either or both measures.

MATERIALS AND METHODS

Ethics Statement

This study was carried out in accordance with the recommendations of and approval by the Oakland University Institutional Review Board. All subjects gave written informed consent in accordance with the Declaration of Helsinki.

Participants

Participants were recruited from social media (e.g., Facebook, Reddit, Twitter) and an undergraduate college population as part of a three-phase online study, whereby each phase tested a different research question related to CNM. A distinct sample of participants was collected for each phase, but participants did have the option of participating in other phases. Data for this study are exclusively from phase 1 of this project. For this phase, we collected a total of 923 responses. To identify whether respondents completed the survey more than once, participants provided anonymous identifiers by indicating (1) the letter of their middle name, (2) the first letter of their mother's first name, (3) the first letter of their sex, (4) the number of the month they were born, and (5) the first letter of their ethnic background. Duplicate participant entries were deleted (*n* = 40) if two or more sets of IP addresses and responses to the anonymous identifier items matched. Participants who completed the survey in <15 min (*n* = 85) were excluded. Participants who indicated they were in an exclusive relationship but were currently involved with more than one person (i.e., non-consensual non-monogamy; *n* = 5) and those who provided inconsistent relationship information (e.g., reported that they were currently involved with only one partner but also indicated 2+ current partners; *n* = 10) were also excluded from analyses.

The final sample consisted of 783 participants (age: *M* = 23.49 years, *SD* = 7.91, range 18–77 years). Participants resided in the United States (91.6%), Europe (4.5%), Oceania (1.9%), Canada (1.7%), Asia (0.1%), South America (0.1%), and Africa (0.1%). Approximately 70% were from Michigan. Participants were asked to identify their biological sex as either male (*n* = 183) or female (*n* = 600), but were also asked to identify their gender (male = 184; female = 579; "other" = 20). Other gendered individuals identified as genderfluid or genderqueer (*n* = 12), agender (*n* = 3), non-binary (*n* = 2), semi-androgynous (*n* = 1), or did not provide a gender identity (*n* = 2). Our sample also contained four transmen and two transwomen. Because our sample of trans and other-gendered individuals was not large enough to conduct separate analyses, biological sex was used for comparisons of sex differences. Participants identified as White (82.6%), Black (6.5%), Asian (4.8%), Hispanic/Latino (1.9%), or Other (4.2%), and reported their sexual orientation as heterosexual (73.8%), bisexual or pansexual (23.2%), homosexual (1.8%), or asexual (0.9%).

All participants reported currently being in a romantic relationship of some type. Following previous methods (Mogilski et al., 2017, 2019), two criteria were used to distinguish between individuals in monogamous, open, and CNM relationships. First, participants reported whether their romantic relationship was exclusive (i.e., you and your partner agree to not date other people) or non-exclusive (i.e., you and your partner(s) agree that dating other people is permitted) and whether they were currently in a romantic and/or physical relationship with only one person or with more than one person. Participants who reported being in an exclusive romantic or physical relationship with only one person were classified as "monogamous." Those who reported being in a non-exclusive romantic or physical relationship with more than one person were classified as "multi-partner." Those who reported being in a non-exclusive romantic or physical relationship with only one person were classified into a third group called "open relationship."

Using these criteria, the sample consisted of 538 monogamous (416 women; age: *M* = 20.65 years, *SD* = 4.70, range = 18–71 years; sexual orientation: 90.0% heterosexual, 8.2% bisexual/pansexual, 1.7% homosexual, 0.9% asexual), 149 multi-partner (117 women; age: *M* = 31.67 years, *SD* = 9.44, range = 18–58 years; sexual orientation: 28.2% heterosexual, 70.5% bisexual/pansexual, 0.7% asexual), and 96 open relationship (67 women; age: *M* = 26.8 years, *SD* = 9.55, range = 18–77 years; sexual orientation: 54.2% heterosexual, 44.8% bisexual/pansexual, 5.2% homosexual, asexual 1.0%) participants. Multi-partner participants reported their current number of partners (48.3% two partners, 26.2% three partners, 20.9% four or more partners), and described their romantic relationships using one or more of the following descriptors:

> (1) "I am in a primary relationship with one person (i.e., an emotional/sexual relationship characterized by a high degree of commitment, shared life goals, and affection) and in secondary relationships with one or more other people (i.e., close, ongoing emotional/sexual relationship(s), but with a lesser degree of commitment than a primary relationship)" (*n* = 93).
>
> (2) "I am equally involved with only two people" (*n* = 31).
>
> (3) "I am equally involved with more than two people" (*n* = 13).
>
> (4) "I am involved in a poly 'web', 'family', or 'intimate network' (i.e., a social web resulting from having romantic relationships among you, your romantic partners, their romantic partners, and so forth)" (*n* = 46).

Monogamous and open participants did not report involvement in any of these relationship structures.

Materials and Procedures

All measures were presented using the online survey program Qualtrics. The order in which participants completed each set of measures was randomized across and counterbalanced within tasks. Informed consent was obtained from all individual participants included in the study. After providing informed consent, participants answered questions about themselves, including a demographic questionnaire (age, gender, race/ethnicity, and sexual orientation), and completed self-report measures of life history, pubertal development, sociosexual orientation, perceived vulnerability to disease, and risk-taking.

Life History

We measured overall life history strategy using the Mini-K (Figueredo et al., 2006; 20 items; α = 0.758) and the HKSS (Giosan, 2006; 22-items; α = 0.842). The Mini-K assesses several domains of social and sexual behavior, including an individual's contact with and support from family, friends, and community (e.g., "I often get emotional support and practical help from my friends/community"); their relationship quality with biological relatives (e.g., "while growing up, I had a close and warm relationship with my biological mother/father"); their capacity for insight, planning, and self-control (e.g., "I often make plans in advance"); and their preference for intimacy and sex with multiple romantic partners (e.g., "I would rather have one than several sexual relationships at a time"; anchors: 1 = strongly disagree, 7 = strongly agree). The HKSS similar assesses life history qualities such as health and attractiveness (e.g., "I don't have major medical problems," "I am in good physical shape"), upward social mobility (e.g., "My training and experience are likely to bring me opportunities for promotion and increased income in the future"), social capital (e.g., "If something bad happened to me, I'd have many friends ready to help me"), and risk avoidance (e.g., "I live in a comfortable and secure home"; anchors: 1 = strongly disagree, 5 = strongly agree). Higher average scores on both measures indicate a slower life history strategy.

Sociosexual Orientation

Two attitudinal aspects of sociosexual orientation were measured using items from the MMSO (Jackson and Kirkpatrick, 2007; α = 0.643): (1) short-term mating orientation (STMO; 10 items, e.g., "I can easily imagine myself being comfortable and enjoying 'casual' sex with different partners") and (2) long-term mating orientation (LTMO; seven items, e.g., "I am interested in maintaining a long-term relationship with someone special"; anchors: 1 = strongly disagree, 7 = strongly agree). Higher average scores on both measures indicate greater preference.

Pubertal Development

Pubertal timing was measured by asking participants to recall whether they had experienced pubertal events relatively earlier or later than their same-sex peers (e.g., changes in voice pitch, facial skin clarity, body hair development; Petersen et al., 1988). Some items were different for men and women depending on their sex-specificity (e.g., "do you think you started having wet dreams earlier or later than your peers?," "do you think your first period was any earlier or later than most other girls?"; anchors: 1 = much earlier, 5 = much later). Participants could report "I don't know." These responses were excluded from analyses. Higher average scores indicate delayed sexual maturation.

Perceived Vulnerability to Disease

Chronic concerns about susceptibility to infectious disease transmission were assessed using the PVDS (Duncan et al., 2009; 15 items) which measures two domains: perceived infectability (e.g., "I am more likely than the people around me to catch an infectious disease"; α = 0.85) and germ aversion (e.g., "I dislike wearing used clothes because you do not know what the last person who wore it was like"; α = 0.77; anchors: 1 = strongly disagree, 7 = strongly agree). Higher average scores indicate greater perceived vulnerability.

Risk-Taking

Attitudes to various risk-taking behaviors were measured using the *Domain Specific Risk-Taking* (DOSPERT; Blais and Weber, 2006; 30 items; α = 0.824) questionnaire. This questionnaire evaluates how likely a participant believes they are to take risks across five domains: *Ethical* (e.g., "passing off somebody else's work as your own"; α = 0.64), *Financial* (e.g., "bettering a day's income at a high-stake poker game"; α = 0.75), *Health/Safety* (e.g., "engaging in unprotected sex"; α = 0.58), *Recreational* (e.g., "going down a ski run that is beyond your ability"; α = 0.79), and *Social* (e.g., "speaking your mind about an unpopular issue in a meeting at work"; α = 0.66; anchors: 1 = extremely unlikely, 7 = extremely likely). Higher average scores indicate greater risk-taking propensity.

RESULTS

All *post hoc* tests were Bonferroni corrected. Their adjusted *p*-values are reported. Because monogamous, open, and multi-partner participants significantly differed by age, $F(2,774) = 176.09$, $p < 0.001$, $\eta_p^2 = 0.31$), we ran our analyses both including and excluding age as a covariate. Patterns of significance were the same in both sets of analyses. Analyses excluding age as a covariate are reported.

Life History Measures

Mini-K

A 2 (participant sex) × 3 (relationship type) between-subjects ANOVA compared scores on the Mini-K among women and men within each relationship type. There was a main effect of participant sex, $F(1,777) = 12.98$, $p < 0.001$, $\eta_p^2 = 0.02$, such that men reported lower scores (i.e., a faster life history strategy; $M = 4.99$, $SD = 0.72$) than women ($M = 5.26$, $SD = 0.69$), and a main effect of relationship type, $F(2,777) = 32.67$, $p < 0.001$, $\eta_p^2 = 0.08$. Participants in multi-partner ($M = 4.81$, $SD = 0.58$, $p < 0.001$) and open ($M = 4.93$, $SD = 0.80$, $p < 0.001$) relationships reported lower scores than monogamous participants ($M = 5.36$, $SD = 0.66$). There was no significant difference between those in multi-partner and open relationships ($p = 0.539$) and no significant interaction, $F(2,777) = 0.05$, $p = 0.949$.

HKSS

A 2 (participant sex) × 3 (relationship type) between-subjects ANOVA compared scores on the HKSS among men and women within each relationship type. There was a main effect of relationship type, $F(2,777) = 4.67$, $p = 0.010$, $\eta_p^2 = 0.01$, such that people in open relationships scored lower (i.e., a faster life history strategy; $M = 3.81$, $SD = 0.53$) than those in monogamous ($M = 3.97$, $SD = 0.46$, $p = 0.007$), but not multi-partner ($M = 3.92$, $SD = 0.40$, $p = 0.124$), relationships. There was a marginally significant main effect of sex, $F(1,777) = 3.59$, $p = 0.059$, $\eta_p^2 = 0.01$, such that men ($M = 3.87$, $SD = 0.47$) scored lower than women ($M = 3.96$, $SD = 0.46$). There was no significant interaction, $F(4,777) = 0.99$, $p = 0.372$.

To assess the construct validity of the Mini-K and HKSS, bivariate correlations were calculated among these scores and the pubertal development, MMSO, PVDS, and DOSPERT scores (**Table 1**).

TABLE 1 | Bivariate correlations among measures of life history (Mini-K and HKSS), male and female pubertal development, risk-taking (DOSPERT), disease avoidance (PVDS), and long- and short-term mating orientations (MMSO).

	HKSS	Mini-K	Male PD	Female PD	MMSO Sh.	MMSO L.
1. HKSS		0.586**	−0.096	0.014	−0.154**	0.186**
2. Mini-K	0.586**		−0.001	0.023	−0.460**	0.344**
3. Male pubertal development	−0.096	−0.001			−0.058	0.089
4. Female pubertal development	0.014	0.023			−0.088*	0.045
5. MMSO short-term	−0.154**	−0.460**	−0.058	−0.088*		−0.324**
6. MMSO long-term	0.186**	0.344**	0.089	0.045	−0.324**	
7. PVDS perceived infectability	−0.164**	−0.011	0.019	−0.027	−0.045	−0.026
8. PVDS germ aversion	0.107**	0.315**	−0.075	0.029	−0.377**	0.213**
9. DOSPERT social	−0.074**	−0.261*	0.036	−0.058	0.371**	−0.168**
10. DOSPERT recreational	0.180**	0.034	−0.148*	−0.012	0.107**	0.082*
11. DOSPERT financial	0.035	−0.004	−0.039	0.018	0.176**	−0.045
12. DOSPERT health/safety	−0.059	−0.187**	−0.098	−0.011	0.336*	−0.028
13. DOSPERT ethical	−0.182**	−0.259**	0.008	0.036	0.426**	−0.155**

	PVDS Inf.	PVDS Ger.	Social	Recreat.	Finan.	Heal./Safe.	Ethical
1. HKSS	−0.164**	0.107**	−0.074*	0.180**	0.035	−0.059	−0.182**
2. Mini-K	0.011	0.315**	−0.261**	0.034	−0.004	−0.187**	−0.259**
3. Male pubertal development	0.019	−0.075	0.036	−0.148*	−0.039	−0.098	0.008
4. Female pubertal development	−0.027	0.029	−0.058	−0.012	0.018	−0.011	0.036
5. MMSO short-term	−0.045	−0.377**	0.371**	0.107**	0.176**	0.336**	0.426**
6. MMSO long-term	−0.026	0.213**	−0.168**	0.082*	−0.045	−0.028	−0.155**
7. PVDS perceived infectability		0.222*	−0.017	−0.095**	−0.032	−0.028	0.032
8. PVDS germ aversion	0.222**		−0.273**	−0.123**	−0.009	−0.232**	−0.173**
9. DOSPERT social	−0.017	−0.273**		0.146**	0.176**	0.228**	0.206*
10. DOSPERT recreational	−0.095**	−0.123**	0.146**		0.280**	0.391**	0.158**
11. DOSPERT financial	−0.032	−0.009	0.176**	0.280**		0.275**	0.404**
12. DOSPERT health/safety	−0.028	−0.232**	0.228**	0.391**	0.275**		0.482**
13. DOSPERT ethical	0.032	−0.173**	0.206**	0.158**	0.404**	0.482**	

***$p < 0.01$. *$p < 0.05$.*

MMSO

Two 2 (participant sex) × 3 (relationship type) between-subjects ANOVA compared STMO and LTMO scores on the MMSO among men and women within each relationship type. For STMO, there was a main effect of sex, $F(1,767) = 32.44$, $p < 0.001$, $\eta_p^2 = 0.04$, such that men ($M = 3.96$, $SD = 1.10$) scored higher than women ($M = 3.16$, $SD = 1.27$). There was also a main effect of relationship type, $F(2,767) = 67.38$, $p < 0.001$, $\eta_p^2 = 0.15$, such that multi-partner individuals scored higher ($M = 4.45$, $SD = 0.86$) than both open individuals ($M = 3.87$, $SD = 1.33$, $p = 0.003$) and monogamous individuals ($M = 2.95$, $SD = 1.19$, $p < 0.001$). Open participants also scored significantly higher than monogamous participants ($p < 0.001$). There was no significant interaction, $F(2,767) = 2.56$, $p = 0.078$, $\eta_p^2 = 0.01$.

For LTMO, there was a main effect for relationship type, $F(2,768) = 52.81$, $p < 0.001$, $\eta_p^2 = 0.12$, such that monogamous individuals scored higher on LTMO ($M = 5.17$, $SD = 0.40$) than those in open ($M = 4.96$, $SD = 0.51$, $p < 0.001$) and multi-partner relationships ($M = 4.61$, $SD = 0.61$, $p < 0.001$). There was also a significant difference between open and multi-partner individuals ($p < 0.001$). There was no main effect of sex, $F(2,768) = 0.90$, $p = 0.343$, nor a significant interaction, $F(2,768) = 1.86$, $p = 0.156$.

Self-Reported Pubertal Timing

Two three-way between-subjects ANOVA compared male and female pubertal timing measures across monogamous, open, and multi-partner relationships. There was a main effect of relationship type for women, $F(2,596) = 5.23$, $p = 0.006$, $\eta_p^2 = 0.02$, but not for men, $F(2,179) = 1.80$, $p = 0.168$, $\eta_p^2 = 0.02$. Women in multi-partner relationships reported earlier pubertal development relative to their peers ($M = 2.79$, $SD = 0.69$) than did women in monogamous relationships ($M = 3.02$, $SD = 0.69$, $p = 0.004$). Women in open relationships ($M = 2.99$, $SD = 0.70$) were not significantly different from women in multi-partner and monogamous relationships.

PVDS

A 2 (participant sex) × 3 (relationship type) between-subjects MANOVA compared scores on the two domains of the PVDS (i.e., perceived infectability and germ aversion) among men and women within each relationship type. For perceived infectability, there was a main effect of sex, $F(1,776) = 21.39$, $p < 0.001$,

η_p^2 = 0.03, such that women perceived themselves as more susceptible to infection (*M* = 3.68, *SD* = 1.40) than did men (*M* = 2.99, *SD* = 1.10). However, there was no main effect of relationship type, *F*(2,776) = 2.00, *p* = 0.136, nor a significant interaction, *F*(2,776) = 2.35, *p* = 0.096.

For germ aversion, there was a main effect of sex, *F*(1,776) = 4.91, *p* = 0.027, η_p^2 = 0.01. Women reported greater aversion to germs (*M* = 3.96, *SD* = 1.16) than men (*M* = 3.56, *SD* = 1.08). There was also a main effect of relationship type, *F*(2,776) = 27.62, $p < 0.001$, η_p^2 = 0.07. People in monogamous relationships reported greater aversion to germs (*M* = 4.13, *SD* = 1.11) than multi-partner (*M* = 3.17, *SD* = 1.02, $p < 0.001$) and open (*M* = 3.46, *SD* = 1.04, $p < 0.001$) individuals. Multi-partner and open individuals were not significantly different from each other (*p* = 0.468). There was also a significant interaction, *F*(2,776) = 3.04, *p* = 0.048, η_p^2 = 0.01. Women in monogamous relationships were more germ averse (*M* = 4.25, *SD* = 1.08) than men in monogamous relationships (*M* = 3.72, *SD* = 1.11), *t*(536) = −4.74, $p < 0.001$, but there were no sex differences within open (women: *M* = 3.28, *SD* = 0.95; men: *M* = 3.54, *SD* = 1.07), *t*(94) = −1.16, *p* = 0.249, or multi-partner (women: *M* = 3.21, *SD* = 0.97; men: *M* = 3.16, *SD* = 1.04), *t*(146) = 0.24, *p* = 0.815, relationships.

DOSPERT

A 2 (participant sex) × 3 (relationship type) between-subjects MANOVA compared scores on the five domains of the DOSPERT among men and women within each relationship type. For each domain, there was main effect of sex (all *F*s > 9.38) such that men scored higher than women on social (*M* = 5.12, *SD* = 1.01; *M* = 4.79, *SD* = 1.02, *p* = 0.001), recreational (*M* = 3.94, *SD* = 1.41; *M* = 3.45, *SD* = 1.40, *p* = 0.002), financial (*M* = 2.75, *SD* = 1.08; *M* = 2.29, *SD* = 0.93, $p < 0.001$), health/safety (*M* = 3.42, *SD* = 1.12; *M* = 2.99, *SD* = 1.08, $p < 0.001$), and ethical risk-taking (*M* = 2.57, *SD* = 1.07; *M* = 2.16, *SD* = 0.83, $p < 0.001$).

There were two main effects for relationship type: social risk-taking, *F*(2,776) = 61.68, $p < 0.001$, η_p^2 = 0.14, and ethical risk-taking, *F*(2,776) = 8.08, $p < 0.001$, η_p^2 = 0.02. People in multi-partner (*M* = 5.56, *SD* = 0.87, $p < 0.001$) and open (*M* = 5.35, *SD* = 0.98, $p < 0.001$) relationships scored higher on social risk-taking than monogamous individuals (*M* = 4.59, *SD* = 0.94). Those in open relationships were not significantly different from multi-partner individuals (*p* = 0.299). Likewise, people in multi-partner (*M* = 2.51, *SD* = 0.89, *p* = 0.007) and open (*M* = 2.43, *SD* = 1.02, *p* = 0.005) relationships scored higher on ethical risk-taking than did monogamous people (*M* = 2.15, *SD* = 0.87), and there were no differences between multi-partner and open individuals (*p* = 1.00).

Finally, there was a significant interaction for ethical risk-taking, *F*(2,776) = 3.40, *p* = 0.034, η_p^2 = 0.01. Men scored significantly higher than women on ethical risk-taking within monogamous, *t*(536) = 4.28, $p < 0.001$, and open relationships, *t*(94) = 3.88, $p < 0.001$, but not multi-partner relationships, *t*(146) = 0.84, *p* = 0.403. All other main effects and interactions were not significant (all *F*s < 2.67, all *p*s > 0.069).

DISCUSSION

We compared self-report indices of life history across men and women within monogamous, open, and multi-partner romantic relationships. Collectively, our results suggest that pursuit of CNM is associated with a faster life history strategy. Individuals within open and multi-partner relationships reported lower scores (i.e., a faster life history) on the Mini-K than those in monogamous relationships. Open individuals also reported lower scores on the HKSS than both monogamous and multi-partner individuals, who were no different from one another.

That individuals within CNM relationships report a faster life history makes sense in light of previous research on the association between faster life histories and promiscuous mating systems. CNM individuals' preference for multiple sexual and romantic partners has been documented across several samples (Morrison et al., 2013; Rodrigues et al., 2016, 2017, 2019; Mogilski et al., 2017, 2019; Balzarini et al., 2018b) and is replicated again in this study using an alternative measure of sociosexuality (i.e., the MMSO) that separately measures affinity toward short- and long-term partnerships. We found that those in multi-partner relationships reported a more STMO than those in open and monogamous relationships, and open individuals reported a more STMO than monogamous people. Interestingly, those in multi-partner relationships also reported less interest in long-term committed romantic relationships than monogamous, but not open, individuals. It is possible that CNM individuals, and particularly those that maintain several concurrent romantic relationships, form fewer enduring partnerships than those in monogamous relationships. However, this is not consistent with prior research. Séguin et al. (2017) found that individuals within polyamorous relationships reported longer relationships than those in monogamous and open relationships, and all three relationship types reported similar levels of partner commitment. Similarly, Mogilski et al. (2017) compared relationship length between monogamous and CNM individuals' primary and secondary relationships. Although they found that monogamous relationships tended to be older than secondary relationships, CNM primary relationships tended to be older than monogamous relationships. This suggests that those in CNM relationships regularly form long-term enduring relationships but are perhaps selective about with whom they maintain those relationships. That is, people who form multi-partner relationships may desire and actively seek a variety of intimate partners, but only maintain partnerships if they are of high quality. Balzarini et al. (2017) reported that primary partnerships tend to entail more commitment than secondary partnerships, and Mitchell et al. (2014) likewise found that polyamorous individuals report greater commitment to one partner than the other. Alternatively, LTMO may differ across different types of CNM. We did not collect data to distinguish different types of multi-partner relationships, but individuals interested in polyamory (i.e., multiple emotionally intimate relationships) may be more oriented toward long-term relationships than those interested in exclusively sexual extradyadic relationships.

Our complementary findings suggest that life history differences between monogamous and CNM individuals extend beyond sociosexuality. Women within multi-partner, but not open, relationships reported earlier sexual debut than women within monogamous relationships. There were no differences in self-reported pubertal timing among men. This is consistent with research showing that early sexual maturity is associated with a faster life history in women (Byrd-Craven et al., 2007; James et al., 2012; also see Hehman and Salmon, 2019), particularly within western industrialized societies (Sear et al., 2019). Scores on the PVDS also revealed that individuals within CNM and monogamous relationships did not differ in their perceived infectability. However, monogamous individuals reported greater germ aversion than both multi-partner and open individuals, while the latter were equally averse. This is consistent with work showing that those who score higher on the Mini-K (i.e., slow life history) report greater pathogen, sexual, and moral disgust than those who score lower (Frederick et al., 2018). For slow strategists, this aversion may motivate protective avoidance of risks that threaten long-term well-being. For fast strategists, a higher threshold for disgust would allow them to capitalize on opportunities despite possible risks (e.g., exposure to disease, interpersonal exploitation). However, these individuals may likewise fail to avoid sexual disease risk, which may become a community health issue. Finally, we also observed that those in multi-partner and open relationships scored higher than monogamous people on social and ethical (though not health) risk-taking. This suggests that CNM individuals may be more likely to disregard how their behaviors are perceived by or affect the well-being of others, but supports research showing that those in CNM relationships tend to be conscientious about sexual health (Conley et al., 2012, 2013b). Collectively, these findings suggest that differences in life history between monogamous and CNM individuals do not merely reflect differences in sociosexuality. Rather, people who are interested in pursuing a CNM relationship may be predisposed to a faster life history strategy.

CNM, Morality, and Sexual Ethics

Knee-jerk condemnation of CNM can produce wrongful discrimination that harms personal and community well-being. For instance, those in CNM relationships typically report being more secretive about their non-primary (or pseudo-non-primary) partners (Balzarini et al., 2019), presumably to avoid third-party punishment. Indeed, Conley et al. (2012) found that women who fear condemnation are less willing to accept an offer of casual sex that they would otherwise enjoy pursuing. This fear of judgment can cause anxiety that prevents those who practice CNM from seeking sexual health services (e.g., STD testing), particularly within rural communities where reputation can be more easily tracked (Kirkman et al., 2015). Moreover, therapists and clinicians who assume that monogamy is a universal relationship ideal may inadvertently marginalize or mistreat patients who are oriented toward multi-partner mating (see Finn et al., 2012; Brandon, 2016; van Tol, 2017; Cassidy and Wong, 2018). In fact, Schechinger et al. (2018) found that CNM individuals reported that therapy was more helpful when therapists were more affirmative about their relationship structure (e.g., did not make an issue of their relationship structure when it was not relevant).

It is possible that moral stigma toward CNM (see Moors et al., 2013) stems from aversion to the high-risk, competitive interpersonal strategies that are characteristic of a fast life history (see Wang et al., 2009; Figueredo and Jacobs, 2010; Kruger, 2010; Griskevicius et al., 2011). Commitment to a faster life history strategy can lead to greater risk-taking (Hampson et al., 2016; Mishra et al., 2017), impulsivity (Frankenhuis et al., 2016; Maner et al., 2017), and aggression against others (Figueredo et al., 2018). Also, robust indicators of faster life history, such as paternal absenteeism and adolescent fertility, predict national rates of criminal violence (Minkov and Beaver, 2016), child maltreatment, and homicide (Hackman and Hruschka, 2013). Moral condemnation of multi-partner mating may thereby occur when condemners believe that monogamy prevents competitive contests for mates, enhancing cooperation within groups and reducing negative physical and mental health outcomes. In other words, though fast life history traits can help individuals cope with an unpredictable environment (Figueredo and Jacobs, 2010; Frankenhuis et al., 2016; Young et al., 2018), they may conflict with the optimal social strategy pursued by slow life history strategists. Baumard and Chevallier (2015) argue that fast life history behaviors may be moralized to the extent that slow strategists promote cooperation, self-regulation, and restricted sociosexuality, and condemn "fast" behaviors such as selfishness, conspicuous sexuality, and materialism. By espousing moral values that promote delayed gratification, sexual monogamy, and altruism, slow life history strategists may condemn multi-partner mating to create stable, cohesive communities that invest in long-term reciprocity and extended prosociality.

Although our data support the conclusion that CNM is associated with fast life history traits, it is important to note that our study assesses dispositional tendencies and not how these tendencies are modified by cultural practices within the CNM community. People who prefer multi-partner mating may have a proclivity toward pursuing a faster life history, but most modern CNM communities have well-developed guidelines for pursuing multi-partner relationships safely and ethically (see Anapol, 1997; Wosick-Correa, 2010; Deri, 2015; Hardy and Easton, 2017). Sexual ethics within CNM communities, including effective birth control methods, may help manage and diminish the traditional costs of competitive, high-risk, promiscuous mating environments. CNM individuals take precautions to attenuate distress caused by a partner's extradyadic involvement (Jackson and Scott, 2004; McLean, 2004; Visser and McDonald, 2007). Those in CNM relationships are just as (or more) likely to practice safe sexual practices than people in monogamous relationships (Conley et al., 2012, 2013b; Lehmiller, 2015). They are also expected to practice open communication, honesty, emotional intimacy, and consent-seeking to reduce the threat of partner defection or resource diversion. Scoats and Anderson (2019) interviewed men and women who engaged in mixed-sex threesomes and found that open communication reduced feelings of exclusion. Similarly, Aguilar (2013) studied two communal living groups practicing polyamory and reported that both cultures discouraged aggression and competition among males within the community.

By reducing the social anxiety that accompanies multi-partner competition, individuals within CNM relationships may experience relationship and health outcomes on par with (or better than) those who pursue monogamy. Those within multi-partner relationships that include ethical treatment of and consent among partners typically experience more positive relationship and health outcomes than those who pursue non-consensual non-monogamy (i.e., adultery; Levine et al., 2018). Compared to those in monogamous relationships, CNM individuals report experiencing less emotional jealousy (Mogilski et al., 2019), and spend less time actively trying to retain their mate (Mogilski et al., 2017, 2019), which may alleviate conflict in relationships where one or both partners desire extradyadic intimacy. Indeed, people with an unrestricted sociosexuality report greater satisfaction within CNM relationships than they do in monogamous relationships (Rodrigues et al., 2016; Fairbrother et al., 2019), and report less preoccupation with constraining relationship forces (i.e., feeling obligation rather than desire toward a partner), which is associated with greater self-reported quality of life (Rodrigues et al., 2019). Stults (2018) also found that gay and bisexual men involved in multi-partner mating reported that the conflict resolution strategies of CNM improved their relationship satisfaction, communication, and trust. This suggests that CNM may improve, rather than dissolve, cooperation and well-being within certain populations – a feature that should be valued by those who fear how public acceptance of CNM might affect social cohesion.

Limitations and Future Directions

The most notable limitation of this research is that it does not assess the influence of measured morality or sexual ethics on behavior within CNM relationships, and these are constructs that should be examined further in future work. Our results should not be interpreted as support for condemnation against CNM. Rather, our data highlight how those with a proclivity toward CNM may possess personality traits that predispose them to take risks, pursue multi-partner mating, and disregard pathogens. CNM may therefore not foster these traits, but rather provide an environment where people can ethically express them. Without strict ethical guidelines for how to handle multiple concurrent romantic relationships, people may pursue multi-partner mating in a manner that produces social disharmony. For example, in sub-Saharan and Muslim populations where polygamy is socially acceptable, women in polygamous relationships experience more spousal mistreatment, abuse, and mental health concerns than those in monogamous relationships (Hassouneh-Phillips, 2001; Özer et al., 2013). Children from these polygynous families also report more mental health and social difficulties, poorer school achievement, and poorer paternal relationships than those from monogamous families (Al-Krenawi et al., 2002; Al-Krenawi and Slonim-Nevo, 2008). Within these populations, these negative outcomes seem to arise when there is competition, hostility, jealousy, and little communication among partners. However, when effort is invested into building respectful and congenial relationships among partners, these outcomes improve (Al-Krenawi, 1998). This suggests that the dynamic of a multi-partner relationship may be a better predictor of relationship functioning than its structure (Elbedour et al., 2002). CNM ethical practices may likewise reduce conflict among those who pursue multi-partner relationships. Specifically, CNM's culture of compassionately enforced sexual ethics may provide an outlet for fast life history strategists to pursue their preferred strategy in a manner that reduces its negative impact on others' well-being.

This research highlights the need to identify and quantify a formal taxonomy of CNM ethics. Although a number of popular guides exist (e.g., Anapol, 1997; Hardy and Easton, 2017), there is no unified scientific examination of the diverse strategies that CNM practitioners use to manage multi-partner relationships. The most obvious ethical guideline that differentiates CNM from other forms of non-monogamy is its namesake: consent. However, this is too broad a concept to capture the myriad of ethical considerations that may arise within a multi-partner relationship. For example, Peoples et al. (2019) presented case studies of two married men who pursued extramarital partnerships with and without the consent of their spouse. They documented that both men, regardless of spouse consent, engaged in antagonistic and exploitative relationship practices, such as deception, partner neglect, and divestment from childcare, which subsequently produced relationship conflict. This suggests that consent-seeking is a nominal feature of CNM relationships and that ethical pursuit of multi-partner mating may instead require a multifaceted approach that addresses the diverse array of anxieties and exploitations that can produce suffering within romantic and interpersonal relationships.

It may be fruitful to begin this investigation by examining how CNM practices complement the recurrent, domain-specific adaptive issues that have shaped humans' evolved psychology. Natural selection has shaped psychological adaptations that protect against cuckoldry and partner abandonment (Buss and Schmitt, 1993, 2019), interpersonal exploitation (Buss and Duntley, 2008; Duntley, 2015), and infection by disease (Al-Shawaf et al., 2015; Tybur and Lieberman, 2016). Although these adaptations may have enhanced reproductive success, they do not necessarily enhance well-being (Kováč, 2012), nor may they function optimally within a modern environment (Li et al., 2018). It is possible that the sexual ethics of CNM, paired with modern sexual health technologies, reduce the need for humans to rely on psychological mechanisms of disgust and moral condemnation to regulate sexual risk-taking and other features of a faster life history. For example, proscribing hostility among partners within CNM relationships may reduce intrasexual competition and its consequences on public health (see Kruger, 2010; Tybur et al., 2012). Future research should compare CNM individuals who adhere or not to the ethical principles espoused by the greater community and assess whether adherence tends to improve relationship functioning, particularly among those who have a predisposition to disregard others' well-being.

Another limitation of this study is that it did not examine a complete array of life history traits. It also relies exclusively on self-report measures, which are vulnerable to revisionism and faulty memory. The validity of the Mini-K and HKSS as self-report measures of life history variation is contested (see Dunkel and Decker, 2010; Figueredo et al., 2013, 2015; see also Copping et al., 2014; Richardson et al., 2017), though our complementary measures provide convergent evidence that CNM is associated with a faster life history. Nevertheless, future research should examine a wider collection of behavioral measures of life history within CNM populations and consider which features of a fast life history are most endemic to CNM populations. Research should also address whether life history features are invariant across different CNM populations and subcultures (e.g., swinging vs. polyamory vs. religious polygamy). People within polyamorous relationships are typically viewed as more moral and responsible than those in swinging and open relationships (Matsick et al., 2014). To the extent that polyamorous relationships are defined by multiple close, emotionally intimate bonds, these relationships (and the people within them) may be seen as less socially disruptive. Similarly, we did not assess whether our participants had children, which can substantially shape relationship behaviors and attitudes (e.g., Barbaro et al., 2016; Flegr et al., 2019).

Finally, there are several methodological issues that should be considered when interpreting this data. First, several of our measures had low Cronbach's alphas, including the MMSO and the ethical, health/safety, and social risk-taking facets of the DOSPERT. Similarly, our measure of pubertal development relied on self-report responses, which may be biased by retrospection. Research designs that rely on alternative, well-validated measures of psychological and social functioning (e.g., psychophysiological assessment; social relations modeling) administered within laboratory or naturalistic settings may help to improve the quality of life history and CNM research more broadly.

CONCLUSION

Individuals in CNM relationships were more likely to report a fast life history than those in monogamous relationships. We speculate that this association may explain moral stigma toward CNM insofar as a faster life history is associated with risky, competitive, antagonistic interpersonal behaviors. Those who benefit from maintaining stable, cohesive groups may favor monogamy and condemn CNM to the extent that multi-partner mating can produce transient relationships, social conflict, and disease transmission; although, as noted, these traits do not necessarily describe individuals in modern CNM relationships. Given existing evidence that CNM relationships are not short-lived (Mogilski et al., 2017; Séguin et al., 2017), can improve relationship satisfaction and functioning (Rodrigues et al., 2016; Levine et al., 2018; Stults, 2018; Fairbrother et al., 2019), and are no more likely to involve unsafe sexual practices than monogamous relationships (Conley et al., 2012, 2013b; Lehmiller, 2015), we suspect that moral stigma toward CNM originates from an increasingly defunct intuitive association between sexually promiscuous mating and interpersonally deleterious fast life history traits (Moon et al., 2018). This mismatch (Li et al., 2018) may be driven by modern CNM ethical practices which reduce sources of interpersonal conflict within multi-partner mating systems (e.g., intrasexual competition, jealous anxiety, partner abandonment, child neglect, and disease transmission). Identifying which common CNM practices most effectively minimize these concerns will be the next step in this fruitful line of research.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Oakland University Institutional Review Board. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

All authors contributed to the study design conception and collection of data. JM, VM, and SR organized and analyzed the data. JM wrote the manuscript. LW provided the editorial feedback.

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An Animal Model for Mammalian Attachment: Infant Titi Monkey (*Plecturocebus cupreus*) Attachment Behavior Is Associated With Their Social Behavior as Adults

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Close social bonds are integral for good health and longevity in humans and non-human primates (NHPs), yet we have very little understanding of the neurobiological differences between healthy and unhealthy relationships. Our current understanding of social bonding is grounded in Bowlby's theory of attachment. Work done with human infants and adult couples has suggested that attachment behavior developed in infancy remains stable through development into adulthood. Unfortunately, knowledge of the neurobiological correlates of attachment behavior has been limited due to a lack of animal models with both infant and adult attachments similar to humans. To address this, we measured behavioral responses to separation from their primary attachment figure in infant and adult titi monkeys (*Plecturocebus cupreus*). In Experiment 1, we tested for a linear relationship between the subject's response to separation as an infant and their response to separation as an adult. We found greater decreases in infant locomotor behavior in the presence, as opposed to absence, of their primary attachment figure to be indicative of decreased anxiety-like behavior in the presence, as opposed to absence, of their adult pair mates during a novelty response task. In Experiment 2, we increased our sample size, accounted for adverse early experience, and tested a different outcome measure, adult affiliative behavior. We hypothesized that the level of intensity of an infant's response to separation would explain affiliative behavior with their mate as an adult, but adverse early experience could change this relationship. When we compared infant response to separation to adult affiliative behavior during the first 6 months of their first adult pair bond, we observed a linear relationship for infants with typical early experience, but not for infants with adverse early experience. Infants with a greater change in locomotive behavior between the father and alone conditions were more affiliative with their first adult pair mate. These data support the use of titi monkeys as an appropriate animal model for further investigation of the neurobiology underlying attachment behavior.

Keywords: attachment, pair bond, non-human primate, social bonding, novelty

INTRODUCTION

Both humans and non-human primates (NHPs) rely on close social bonds to survive and thrive in their environments (Berkman and Syme, 1979; House et al., 1988; Holt-Lunstad et al., 2010; Stanton and Campbell, 2014). Consequently, expanding our knowledge of the underlying biology of social bonding is important for understanding the impact social bonds have on mental and physical health outcomes. For humans, common social bonds can take the form of friendships, familial bonds, or romantic partnerships. Infant-parent and adult romantic relationships are further characterized by forms of attachment as described in Attachment Theory (Bowlby, 1969; Hazan and Shaver, 1987). The current article is written from a developmental perspective, but it should be noted that Attachment Theory has been historically discussed within different psychological contexts (for a detailed review see George and West, 1999). For both infant-parent and adult romantic relationships, the attachment is defined by three distinct behaviors: proximity maintenance, distress upon involuntary separation, and the ability of the attachment figure to ameliorate stress during anxiety-provoking instances (Bowlby, 1969; Hazan and Shaver, 1987; French et al., 2018). While these three behaviors are the keystones of attachments and relationships, they vary between and within individuals, reflecting the quality of the bond. Infantile attachment behavior has been extensively studied in non-human animal models, but adult attachment, or pair bonding, is largely unexplored in animal models including NHPs. Developing an NHP model capable of illustrating individual variation in attachment behavior, similar to that in humans, from infancy to adulthood could open opportunities to understand the intricate effects of attachments on behavior, cognition, and biology.

The mother–infant bond has been similarly characterized in non-human animals and humans, with infants categorized as secure, insecure/anxious, or insecure/avoidant (Harlow and Zimmermann, 1959; Bowlby, 1969, Bowlby, 1982; Ainsworth, 1979; Bard and Nadler, 1983; Vaughn and Waters, 1990; Kondo-Ikemura and Waters, 1995; Warfield et al., 2011; Numan, 2015). Adult attachment styles follow similar categories as infant attachment styles and can be measured through self-reports but are usually measured by coding observed interactions between partners (Hazan and Shaver, 1987; Vaughn and Waters, 1990; Slade et al., 1999). Both secure infants and adults exhibit confidence that their caregiver or partner will be available and responsive when needed, as illustrated by robust positive effects of their caregiver or partner's presence during stressful situations and faster physiological recovery from stressful situations (Ditzen et al., 2008; Meuwly et al., 2012). Insecure/anxious infants and partners desire frequent interaction or contact while simultaneously exhibiting emotional distance and a reluctance to express closeness with their caregiver or partner (Ainsworth and Bell, 1970; Waters, 1978; Ainsworth, 1979). Anxiously attached individuals experience greater distress and, at times, increased anger toward their parents or partners in stressful scenarios compared to their securely attached counterparts (Feeney and Kirkpatrick, 1996; Rholes et al., 1999). In adulthood, avoidant and anxious partners exhibit jealousy and emotional extremes (Hazan and Shaver, 1987; Levy and Davis, 1988). In this study, our goal was to develop an NHP model to investigate the physiological and neurobiological processes that underlie these individual differences.

The frequency of infant attachment styles is paralleled in the adult population suggesting that attachment style may remain consistent throughout life (Bartholomew and Shaver, 1998; Fraley, 2002). However, some studies have found inconsistencies between infant attachment behavior and adult attachment styles. Weinfield et al. (2000) noticed an abnormally high distribution of insecure attachment styles in adults from high risk backgrounds, defined by the mother's age, income, and whether or not the pregnancy was planned, compared to estimates from middle class adults without such risk factors. They believe this disparity could be due to high rates of childhood maltreatment and maternal depression. This proposition has been supported by research in animal models of maternal abuse in which the offspring grow up to develop atypical social behavior (Maestripieri et al., 2005; Rincón-Cortés and Sullivan, 2016). Changes in attachment behavior also vary depending on the type of attachment an infant initially develops. Human infants classified as secure, who consequently experience stressful life events are more likely to become insecurely attached as adults than insecure infants experiencing typical experiences are to become securely attached (Waters and Merrick, 2000). Individuals with unstable attachment figures also exhibit more variability in attachment behavior compared to individuals who have stable relationships with their attachment (Jones et al., 2018).

Given the difficulty of tracking human attachment behavior through the lifespan across a multitude of different bonds form from infancy to adulthood (Fraley, 2019), we sought to explore attachment behavior in a New World monkey, the coppery titi monkey (*Plecturocebus cupreus*, formerly known as *Callicebus cupreus*). While a young adult human in their twenties may have already experienced a variety of intimate bonds, titi monkeys in the laboratory offer an opportunity to directly study the relationship between an infant's attachment to their parent and the same subject's attachment to their first mate. Infant titi monkeys form a specific attachment to their fathers, exhibiting distress upon separation, increased exploration in the father's presence, and proximity maintenance (Hoffman et al., 1995; Spence-Aizenberg et al., 2016). Previous work with infant titi monkeys revealed effects of adverse early experience in the response of titi monkey infants to separation from the attachment figure and exposure to a novel environment. Larke et al. (2017) ran a modified open field test in which infant titi monkeys were placed in an open field with the opportunity to move about the new environment freely and engage with a novel object. The infants were then either left alone in the open field or allowed to interact with their mother, father, or sibling through a mesh grate (Larke et al., 2017). Infant titi monkeys with adverse early experience were less likely to maintain proximity to their father and exhibited more exploratory behavior during the separation condition (Larke et al., 2017). This work was the first to show variability in attachment behavior of infant titi monkeys. The current study aims to expand on these findings by examining consistencies in attachment behavior between the father–infant bond and the adult pair bond.

Adult titi monkeys form pair bonds that are similar to those observed in humans and can be summarized by the following behaviors and responses: proximity seeking (contact, preference, and exclusivity), separation distress (increased vocalization rate, heart rate, cortisol, and locomotion), and stress buffering (reduced vocalization rate, heart rate, and cortisol) (Mason and Mendoza, 1998). Behavioral and neurological variation can be observed within the first 48 h of pairing, shifting toward more affiliative behaviors and altered neural activity in the nucleus accumbens and ventral pallidum (Bales et al., 2007). There are also differences in behavioral maintenance of the pair bond, depending on individual temperament. For example, individual variation in aggression has been shown to predict affiliation within a pair. More characteristically aggressive males (which show higher levels of mate-guarding or "jealous" behavior) tended to be less affiliative with their partners (Witczak et al., 2018).

CURRENT STUDY

Experiment 1

The current study examined the relationship between infant attachment behavior and adult attachment behavior in the titi monkey. We collected data on attachment behavior through a variety of measures. Subjects were tested in the presence and absence of their father and mother (as infants), or pair mate (as adults). Based on the Ainsworth Strange Situation paradigm we used a novel situation to provoke a psychological threat to activate attachment systems, measuring the subject's behavior during a father, mother, and an alone condition (Ainsworth and Bell, 1970). We used the modified infant open field (IOF) test from Larke et al. (2017) to examine infant behavior during a novel experience in the presence and absence of their father. We were unable to use an open field task in adults, because they would be able to jump out of the arena. Therefore, adult behavior was assessed with a different novelty response task designed based on previous research showing anxiety-like behavior in response to novelty (Hennessy et al., 1995). During the task, the animals are trained to approach a wire box containing a series of unfamiliar patterns, which range from a blank sheet to complex patterns, and retrieve a piece of banana. The task reliably elicits behavioral inhibition in response to novel patterns (Arias del Razo et al., 2019). Although our infant task differs from our adult task, each paradigm achieves the overarching goal of activating the attachment system through exposure to anxiety-provoking situations (Bowlby, 1982; Simpson et al., 1992).

Given that infant titi monkeys form a primary attachment to their father, we hypothesized that variation in titi infant response to the presence of their father, but not their mother, in the IOF test would be demonstrative of their attachment behavior as adults. Specifically, infants that responded to the sight of their father during the IOF test with increased contact calls, decreased locomotion, and increased time spent at the grate, which are examples of the infant seeking proximity and comfort during a stressful situation, would also receive the most benefit from their partner's presence during the novelty response task as adults (Hoffman et al., 1995). In adulthood, we expected to see similar individual variation in behavioral responses to involuntary separation from their pair mate as we had observed in the IOF test. We hypothesized that the reaction to involuntary separation during the alone condition would inhibit behavioral response during testing. We also hypothesized that individuals that were more affiliative with their pair mate would have a stronger reaction to separation from their pair mate and would therefore be less likely to participate in the task than subjects that showed less affiliation with their pair mate.

Experiment 2

Following Experiment 1, we investigated the relationship between infant behavior, life experience, and adult pair behavior more specifically. We began with the same infant data from subjects' 4-month IOF test but this time we coded any/all adverse experiences the subject experienced during development. We took special note of adverse experiences occurring after the subject's IOF test that may have changed their attachment behavior, but considered all adverse experience when examining group differences because we cannot be certain of when or how these experiences will affect behavior (Opendak and Sullivan, 2016). These data were then entered into a linear model predicting affiliative behavior in the subjects' first adult pair bond. We hypothesized that infants exhibiting strong attachments to their fathers, evidenced by an increased behavioral response to his absence, would also exhibit more affiliative behavior in their first adult pair bond. We also expected to see an effect of adverse experience on this relationship such that behavior in the IOF test would not be adequate explanation of variance in adult affiliative behavior if the infants experienced adversity during development.

MATERIALS AND METHODS

Subjects

Experiment 1

Subjects were 11 captive-born titi monkeys (*P. cupreus*), five males and six females, housed at the California National Primate Research Center (CNPRC) in Davis, California. All subjects were tested at two time points: 4 months of age and adulthood between 27 and 118 months old (mean age = 51.6 months, SD = 34.7 months). Infants were housed in their natal group and once subjects reached adulthood, they were removed from their natal group and housed with an unfamiliar opposite sex pair mate in 1.2 m × 1.2 m × 1.8 m cages. Pairs were determined by the experimenters based on lack of genetic relatedness, to avoid inbreeding in the colony. All animals were housed indoors and fed twice daily at 09:00 h and 13:00 h with water available *ad libitum*. Their diet consisted of a commercial primate chow diet supplemented with rice cereal, carrots, bananas, apples, and raisins. Husbandry training and caging were the same as previously described in Valeggia et al. (1999) and Tardif et al. (2006).

Experiment 2

Subjects were 25 captive-born titi monkeys (*P. cupreus*), 12 males, and 13 females, housed at the CNPRC. All subjects were tested in the IOF test at 4 months of age. Of the 25 subjects, 11 were from Experiment 1. As adults, they were observed every 2 h from 08:30–16:30 h for 6 months following their first pairing (mean age = 26.2 months, SD = 9 months). Subjects were housed and fed identically to Experiment 1. All procedures were approved by the University of California, Davis Institutional Animal Care and Use Committee.

Experimental Design

Infant Open Field

The testing apparatus was made to resemble an open field similar to those used in rodent studies (Gould et al., 2009). The paradigm was adapted for infant titi monkeys with walls constructed 1 m high around a base 1 m wide by 1 m long. Walls were made out of opaque white polyvinyl chloride to limit visibility to the surrounding area. As in rodent open field tests, the floor was marked with gridlines to indicate specific locations within the field. A wire mesh grate was built into one of the walls to allow visual, auditory, and olfactory access to the infant's father or mother. At the start of testing, a small piece of brown felt was placed on the left side of the open field (with respect to the wire grate) to serve as a novel object. A familiar food reward, most often a peanut, was placed on the right side of the open field. The field was illuminated by bright overhead lights.

Testing was conducted between 06:00 and 08:00 h. Subjects and their family members were caught in transport boxes (0.3 m × 0.3 m × 0.6 m in size) made of white opaque plastic and wire mesh. Adults and older siblings were caught in individual boxes while the subject would share a box with one of their family members, most often their father. The transport boxes were then covered with a towel and brought to a separate room to eliminate auditory and olfactory stimuli from other monkeys.

The full test consisted of four randomized trials in which an empty transport box, a transport box with the mother, the transport box with the father, or the transport box with a sibling were placed in front of the grate. If the subject did not have a sibling, they were exposed to the empty transport box for an additional trial. The current study did not analyze infant behavior during the sibling condition, and if the infant did not have a sibling we analyzed the first of the two possible empty conditions to avoid exacerbation of the stress response due to extra time alone in the open field (Larke et al., 2017).

Novelty Response Task

This study employed a within-subjects design with "social" and "alone" conditions counterbalanced. There was a minimum of 3 weeks between testing conditions for all subjects. Both testing sessions were a minimum of 6 months after the subject had been paired. Six months was selected based on previous experiments that show titi monkeys have a consistent behavioral preference for the new pair mate after 6 months of pairing (Rothwell et al., submitted). Average pair tenure for the current subjects was 18.2 months (*SD* = 9 months). The novelty response task was used to assess the ability of a pair-mate's presence to buffer an individual's stress response. Previous work with titi monkeys shows that they are more inhibited and exhibit greater elevations in stress hormones in response to novelty than another, non-monogamous, New World monkey species, the squirrel monkey (*Saimiri sciureus*) (Hennessy et al., 1995). This study also showed that small incremental changes in novelty were enough to evoke an elevated cortisol response in the titi monkey.

For the task, we used a small wire box, hereafter referred to as the test box. The test box contained a card displaying the visual stimulus and a small ledge where a piece of banana reward could be placed. For the animal to have completed the task he/she must have approached the test box and reached toward the visual stimulus to retrieve the reward. Animals were first habituated to the test using a blank card in the testing box. Habituation could consist of up to 15 sessions with 10 trials in each session; however, none of the current subjects needed the maximum number of sessions. Subjects were habituated under both conditions, either alone or social before they were tested in the respective paradigm. To be considered habituated, the animal had to approach the test box and reach for the reward under 30 s for 10 consecutive trials. Once the animal met habituation criteria they began testing.

A single test consists of six trials in which the subject must complete the novelty response task. The difficulty of the task differed depending on which visual stimulus was presented. The six trials consisted of six cards from set of cards: a baseline card, four patterned cards ascending in complexity, and a final baseline card (**Table 1**). For the first and sixth "baseline" trials, the animal was shown a blank white card. During trials 2–5 the animal was shown increasingly complex patterns. An animal's participation on the task was measured by the time it took for the animal to retrieve the reward on each independent trial. The animal was given 30 s to complete the task. Failure to retrieve the reward within that time frame was marked as a "balk" and interpreted as a refusal to participate. All patterns were black and white to control for sex differences in titi monkey color vision (Bunce et al., 2011).

Each card that the animal was exposed to during testing was novel to that individual on the first day of testing. Testing in each paradigm was conducted across 4 days. If, for some reason,

TABLE 1 | Descriptions of visual stimuli presented to the subjects during the novelty response task.

Trial number	Description of card content
Trial 1	Baseline-blank white background
Trial 2	A single line
Trial 3	Three different simple geometric shapes
Trial 4	Two different simple geometric shapes and two drawings of flowers
Trial 5	Eight elements against a background shaded differently than trials 2–4: two intersecting lines, two simple geometric shapes, two slightly more complex geometric shapes, and two drawings of flowers.
Trial 6	Baseline-blank white background

testing could not be completed consecutively, we made sure all four test days occurred within the same week.

For example:

Testing day 1: Card set #1 – six trials
Testing day 2: Card set #1 – six trials
Testing day 3: Card set #2 – six trials
Testing day 4: Card set #2 – six trials.

A total of six card sets were used for the experiment. Each individual was only tested on four of the six sets to ensure there were enough sets for their pair mate to be tested with a novel set during their social condition instead of reusing one that they may have seen by chance when their pair mate was being tested.

Testing was completed in the animal's home cage either in the presence or absence of their pair mate. At the start of each test, the experimenter would enter the cage with a small familiar transport box. If it was the social condition, the experimenter would simply enter and exit the cage with the box in hand. In the alone condition, the experimenter would catch the pair mate in the transport box and take them out of the cage. The pair mate would wait out of sight of the subject. However, the cage mate remained within olfactory and auditory access of the subject and any vocalizations were audible to their pair mate. Once the cage mate had been removed, the test box was clipped to the side of the cage, and the test began. The subject was ushered to the back of the cage while the experimenter placed the card and the banana behind a visual barrier. A trial began with a count down, "3, 2, 1, start", then the experimenter removed the barrier and exposed the designated card. The trial ended when the subject was observed reaching for the banana. If the subject did not reach for the banana within the 30-s time limit, the experimenter covered the card, counted that trial as a "balk," and moved on to the next trial.

Zone Training

For the social condition, the subject and cage mates (some subjects had offspring in the cage) were trained to approach and remain in a designated zone as not to interfere with each other's testing. During training, two experimenters would stand outside the cage and call the animals forward to specific zones. The zones were initially determined based on the apparent preference of each animal. The animal could choose to approach a small perch on the left side of the cage, known to staff as the enrichment perch where they were frequently given enriching foods (grains, rice cereal, and greens), or the animal could approach the right side of the cage where their food bowl was mounted (**Figure 1**).

Once the subject chose a zone, the experimenter would begin positive reinforcement training with a clicker. The goal was to reward the animal each time they observed their cage mate receive a treat while waiting in their own zone. During each session, both animals were trained to participate but only the test subject received the clicker training to avoid confusion with extra click sounds. Once animals showed a readiness to approach their zone and they were willing to remain in the zone for an entire 5-min session, the subject moved on to habituation for the novelty response task.

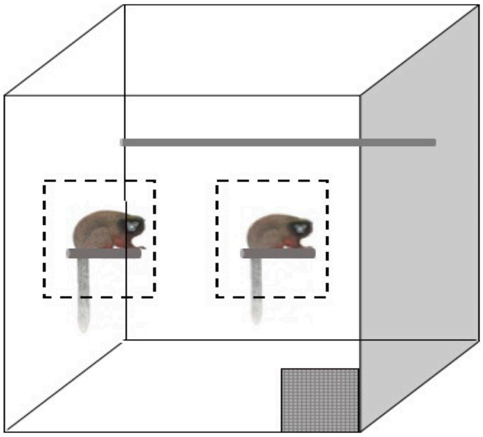

FIGURE 1 | Simplified representation of the titi monkey home cage. The gray checkered box is the release door, the gray cylinder each animal is sitting on represents a perch and trained/testing zones are indicated by dashed outlines. Not to scale.

Affiliation Data

Scan sampling data on affiliation were used to determine baseline levels of affiliation between pairs in this study. These data were collected through cage-side checks, which were performed every 2 h 5 d a week for 6 months before each testing condition. Animals were scored for the following behaviors: contact (any bodily contact between the pair mates), proximity (within one arm's reach of their pair mate), and tail-twining (pair mates sitting side-by-side with their tails wrapped together). If the animals were not engaging in any of these behaviors, they were marked as "none" for that observation. The mean number of checks per day for all subjects was 4.98 with a standard deviation of 1.02.

Values were then calculated for each subject from the pair check data for 6 months prior to testing in Experiment 1 or 6 months after pairing for Experiment 2. The values are the mean ratio calculated by dividing the number of observations the pair was observed in contact or proximity by the total number of observations that day. One of our subjects did not have a tail, due to necessary medical intervention, so we decided not to compare tail twining behavior for any of our subjects. Contact and proximity values (Exp. 1 M = 0.36, SD = 0.08; Exp. 2 M = 0.21, SD = 0.09), calculated from an average of 558 observations, indicate the percentage of scan samples participants were observed in contact or proximity each day, respectively.

Adverse Early Experience Classification

Infant experience was classified as adverse similar to Larke et al. (2017). We classified infant experience as adverse if the infant experienced a loss of a parent, a traumatic injury, or a significant separation from their attachment figure sometime before 9 months of age. We chose 9 months because that is the typical age our laboratory observes the infant behaving completely independent; behaviorally, the infant is no longer nursing or clinging to a parent.

Data Analysis

Infant Open Field

For IOF behavior we analyzed all 25 subjects from Experiments 1 and 2 together. All locomotion, grate touch, and grate zone data were scored using Behavior Tracker 1.5[1]. The current study used the same ethogram as Larke et al. (2017) for measures of locomotor behavior (i.e., gridline cross) and proximity seeking behavior (i.e., grate touch and grate zone positioning). High levels of locomotor behavior are interpreted as increased arousal and high levels of proximity seeking behavior are indicative of the infant attempting to approach the stimulus on the other side of the grate. According to the Shapiro–Wilk normality test frequency of gridline crosses was not normally distributed in our sample ($W = 0.78$, $p < 0.001$). We scored the number of vocalizations each subject emitted during testing RavenLite2.0 (Bioacoustics Research Program 2014, Ithaca, NY, United States) software. Vocalization frequency data were normally distributed ($W = 0.98$, $p = 0.23$) with high levels of vocalization indicating increased arousal and proximity seeking behavior.

To account for non-normal data, we chose to run a linear mixed model (LMM) based on its robustness to abnormal distributions (Arnau et al., 2012) in R Statistical Software (version 3.2.2, R Core Team, 2018). Considering infant titi monkeys' primary attachment to their father, we did not initially include infant behavior from the mother condition in our analyses. Our full model examined changes in behavior from the empty condition to the father condition and whether sex or the order of the condition in which the subject was exposed to first altered their behavior (fixed effects) with subject ID and day of testing as a random effect to account for repeated measures. After running our model, it became clear that there were no significant interactions or effects of sex, order of test condition, or day on behavior; we therefore elected to collapse the data set so that there was only one value per subject per behavior per condition (the mean value across all test days). The condensed data were normally distributed ($W = 0.95$, $p = 0.19$) and we performed one-way ANOVA's with Tukey's honestly significant difference (HSD) *post hoc* compare behavior between conditions.

Participation in the Novelty Response Task by Trial

All data were analyzed using R Studio (R Core Team, 2018). A Shapiro–Wilk test for normality revealed a heavy right skew in the latency data (Royston, 1982). The skew in the data was due to a right censorship of data where subjects balked. To account for the skew in the data we transformed the data into a binomial distribution indicating whether or not a subject participated in the given amount of time. To examine the effects of trial on participation behavior we ran a generalized LMM with trial condition as fixed effects and subject ID as a random intercept. Using emmeans package in R studio (version 3.2.2, R Core Team, 2018) we compared the estimated marginal means of each trial to determine which were statistically significant. These *post hoc* comparisons were done with pairwise, two-tailed, *t*-tests.

Experiment 1

To examine the effects of condition, affiliation with pair mate (measured by observed contact and proximity), order of condition, and sex on percent of participation in: all trials combined, easy trials (levels 1, 2, 3, and 6), and hard trials (levels 4 and 5), we calculated an average percentage of participation across all 4 days of testing to transform the data to continuous variables for a LMM. Trial types were identified as easy or hard by previous models comparing subject participation in each trial. Full models included the fixed effects: testing condition, order of condition, sex, pair experience (whether or not this was the subject's first pair mate), order of conditions by type of condition interaction, sex by type of condition interaction, pair experience by condition interaction, and an order by condition interaction. To account for repeated measures all models included subject ID as a random intercept. We used a combination of backward selection and a loglikelihood ratio test combined with comparisons of Akaike information criterion (AIC) values to ensure we had the most parsimonious model (**Supplementary Tables S1A,B**). None of our independent variables explained more variance in participation during easy trials than the null hypothesis so they are not reported.

To remain consistent with our *a priori* model we included condition and affiliation scores in our final model regardless of whether they explained a significant amount variance. We constructed our *a priori* model from previous knowledge of affiliation and separation behavior in socially bonded species and hypothesized that the degree to which subjects express affiliation or respond to separation would relate to their behavioral response to separation from their pair mate (Ditzen et al., 2008).

For participation by infant behavior during father and empty conditions, data were analyzed similarly to our analysis of test condition with the addition of infant behaviors from our 11 subjects as independent variables. Based on *a priori* hypotheses, we only analyzed participation during the most difficult trials of the task which we believed most likely to activate the attachment system. Our full model contained infant locomotor, vocalization, grate zone, and grate touch behaviors as well as test condition and sex as fixed effects. We also included interaction terms between all infant behavior and test condition in anticipation that infant behavior would differentially explain adult participation depending on the condition. We then systematically removed insignificant effects through backward selection until we had the most parsimonious model with the lowest AIC value (**Supplementary Table S1C**). For participation by infant behavior during mother and empty conditions, we ran the same models as with the father condition with the exception of vocalization behavior (**Supplementary Table S1D**).

Experiment 2

To examine whether variability in adult affiliation could be explained by adverse early experience, we ran a linear regression with adverse early experience (yes or no) as the independent variable and adult affiliative behavior as the dependent variable. Adult affiliative behavior was defined as either the proportion of time the pair was observed in contact, or a combination

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[1] www.behaviortracker.com

of contact and proximity over the first 6 months of their first adult pair bond.

To test a possible relationship between infant behavior and adult affiliation we utilized linear regression starting with a full model containing all four measured infant behaviors (locomotion, vocalizations, grate touch behavior, and grate zone behavior) along with their interactions with IOF testing condition. We ran Shapiro–Wilk tests to confirm all four independent variables were normally distributed. We then selected the model with the smallest residual sum of squares for further interpretation.

RESULTS

Infant Open Field

There were significant effects of condition on all observed behaviors regardless of which order the trials were presented. We did not observe any sex differences in infant behavior. Order and sex were therefore removed from the model due to non-significance. We elected to collapse the data set so that there was only one value per subject per behavior per condition (the mean value across all test days), and we performed independent sample's t-tests to compare behavior between conditions.

One-way ANOVA followed by Tukey's HSD *post hoc* comparisons revealed a significant difference between infant behavior in the father condition and the empty condition for all four behaviors. Subjects crossed more gridlines in the empty condition than in the father condition [$t(39) = 3.26$, $p = 0.001$], vocalized less in the empty condition than in the father condition [$t(48) = -5.46$, $p < 0.001$], spent less time touching the grate and in the grate zone in the empty condition than in the father condition [$t(43) = -3.10$, $p = 0.002$ and $t(48) = -3.87$, $p < 0.001$, respectively] (**Table 2** and **Figure 2**).

Novelty Response Task

Our generalized LMM containing trial and condition as fixed effects with subject ID as a random intercept significantly outperformed the null ($\chi^2 = 41.17$, $p < 0.001$). This model revealed a significant decrease in participation for trials 4 and 5 ($Z_{528} = -3.06$, $p = 0.03$ and $Z_{528} = -3.97$, $p = 0.001$, respectively) compared to participation for trial 1. Participation was also significantly lower in trial 5 compared to trials 2, 3, and 6 ($Z_{528} = -3.75$, $p = 0.002$, $Z_{528} = -3.57$, $p = 0.005$, and $Z_{528} = -2.95$, $p = 0.04$, respectively). The raw number of balks, instances where the monkey did not perform the task, by trial can be seen in **Figure 3**. We also saw an effect of social condition on task participation such that subjects were 1.9 times more likely to participate during the social condition than when they were alone ($Z_{528} = 2.01$, $p = 0.05$).

TABLE 2 | Mean and standard errors for our 25 subjects' behavior across all 3 days of IOF testing.

Behavior	Condition	Mean	SE
Locomotor behavior (gridline crosses)	Empty	85.5	11.35
	Father	48.5	8.03
	Mother	72.8	11.39
Vocalizations	Empty	115.54	8.65
	Father	162.8	6.12
Grate touch (in seconds)	Empty	54.7	12.37
	Father	93.1	8.75
	Mother	82	12.42
Grate zone (in seconds)	Empty	139	15.35
	Father	199	10.86
	Mother	183	15.41

Experiment 1

Participation in Novelty Response Task Trials by Adult Affiliation

Participation across all six trials

According to AIC scores and log likelihood comparisons, our final and most parsimonious model to explain novelty response task participation by condition and affiliation for all six trials combined and easy trials only included condition, affiliation (both contact and proximity measures), pair experience, and four interaction terms (condition by pair experience, condition by order, condition by contact, and condition by proximity) as fixed effects with subject ID as a random intercept to predict task participation (**Supplementary Table S1A**). With the current data we were unable to explain the variability in overall novelty response task participation with our hypothesized variables.

Participation during easy trials

Similarly, none of our models examining variance in participation during easy trials of the task outperformed the null (**Supplementary Table S1B**). Subject participation during easy trials does not appear dependent on testing condition or pair affiliation.

Participation during difficult trials

For difficult trials only, our final model included condition, affiliation (both contact and proximity measures), pair experience, and two interaction terms (condition by pair experience and condition by proximity) as fixed effects with subject ID as a random intercept to predict task participation (**Supplementary Table S1C**). Due to the small sample size, the expected variability from sample to sample was such that we cannot say that test condition explained more of the variance in our data than the null model [$b = -19.00$, CI 95% = (−74.672, 38.015)], ($t_{88} = -0.70$, $p = 0.51$) (**Table 3**). However, we did observe an effect of contact on participation with pairs observed in contact most often participating less in the novelty response task overall [$b = -244.36$, CI 95% = (−481.162, 12.183)], ($t_{88} = -2.18$, $p = 0.048$) (**Table 4** and **Figure 4**).

Adult Task Participation by Infant Behavior With Dad

After backward selection and AIC model comparisons, our final model explaining the relationship between adult task participation and infant behavior consisted of: infant locomotor behavior, vocalizations, grate touch and grate zone behavior, test condition, and the interactions between test condition and all infant behaviors as fixed effects, with subject ID as a random intercept (**Supplementary Table S1D**). Infant sex and vocalizations did not explain a significant portion of variability in adult participation in the difficult trials of the novelty response

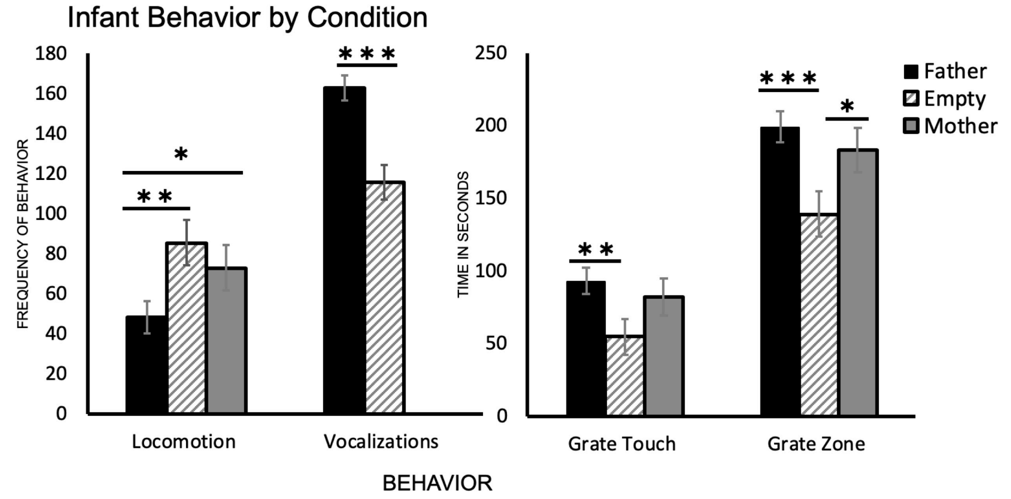

FIGURE 2 | A summary of each infant behavior ($N = 25$) by condition. Locomotion represents the number of times an infant crossed a gridline, vocalizations are a count of all infant vocalizations during the trial, and grate touch plus grate zone behaviors are measured in seconds (total time per trial was 300 s). $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

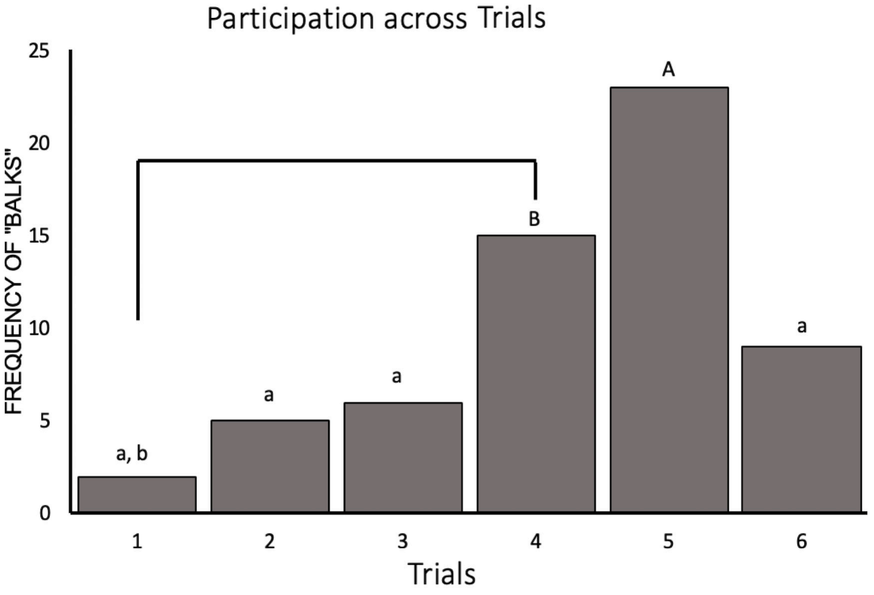

FIGURE 3 | Novelty response task participation ($N = 11$) represented by the frequency of "balks" (i.e., instances where the animal refused to participate) plotted by trial. Trials labeled with a lower case "a" are significantly different from trial 5 ("A") and trials labeled with a lower case "b" are significantly different from trial 4 ("B").

task. Our model showed an interaction between infant locomotor behavior and condition such that infant locomotion during the father condition explained a significant amount of the variance in participation during difficult trials of the novelty response task when their partner was present [$b = -0.64$, CI 95% = (1.37, −0.01)], ($t_{528} = -2.60, p = 0.03$) (**Table 4**). Infants that locomoted less when their father was present were more likely to participate in the difficult trials of the novelty response task when their partner was present as adults (**Figure 5**). We identified one potential outlier in our dataset and ran the same model without this value to investigate its effect on our observed associations. After excluding the data point with the highest frequency of gridline crosses, we were unable to explain variability in adult task participation. However, there was no theoretical reason to exclude this data point, so our following analyses will refer to the model including all observations.

Adult Task Participation by Infant Behavior With Mom

To confirm that this effect was related specifically to attachment behavior rather than general temperament, we ran the same model with infant locomotor behavior when their mother was present instead of their father. This model did not outperform

TABLE 3 | Summary of results for Experiment 1.

Predictor	Outcome	β	SE	p
Adult affiliative behavior	*Novelty response task participation during difficult trials*			
Social condition		−19.00	27.34	0.51
Pair experience		30.36	16.35	0.09
Proportion of contact with mate		**−244.36**	**112.22**	**0.05**
Proportion of proximity with mate		88.25	96.27	0.38
Social condition * pair experience		−24.55	18.94	0.23
Social condition * proportion of contact with mate		−26.16	125.15	0.84
Social condition * proportion of proximity with mate		145.03	110.77	0.23

Multiple linear regression model (N = 11) characterizing adult participation in the novelty response task from adult affiliative behavior. Boldface indicates statistically significant predictors.

TABLE 4 | Summary of Experiment 1.

Predictor	Outcome	β	SE	p
Infant behavior during father condition with empty condition as the reference	*Novelty response task participation during difficult trials*			
Adult social condition		35.16	52.20	0.52
Infant grate touch behavior (Dad)		−0.41	0.25	0.13
Infant grate zone behavior (Dad)		0.41	0.22	0.09
Infant vocalizations (Dad)		−0.15	0.17	0.40
Infant locomotor behavior (Dad)		−0.22	0.11	0.08
Social condition * infant grate touch behavior		0.34	0.25	0.22
Social condition * infant grate zone behavior		−0.52	0.24	0.08
Social condition * infant vocalizations		0.38	0.31	0.25
Social condition * locomotor behavior		−**0.52**	**0.24**	**0.03**

Multiple linear regression model (N = 11) characterizing adult participation in the novelty response task from behavior in the father infant open field conditions. Boldface indicates statistically significant predictors.

the null suggesting infant behavior when their mother is present does not account for variability in adult behavior [$b = 39.31$, CI 95% = (−0.61, 87.04)], ($t_{528} = 2.08$, $p = 0.07$). There were also no interactions between locomotor behavior and condition [$b = -0.24$, CI 95% = (−0.45, −0.01)], ($t_{528} = -2.09$, $p = 0.08$). However, our model with infant behavior during the mother condition as an explanatory variable of adult participation in the novel pattern task did reveal some interesting effects. In the current sample, infants that tended to spend more time spent in the grate zone when their mother was present participated more in the difficult trials of the novelty response task [$b = 0.44$, CI 95% = (0.04, 0.85)], ($t_{528} = 2.44$, $p = 0.04$) (**Table 5**). There was also an interaction between grate touch behavior and adult participation indicating that infants that spent less time touching the grate when their mom was present participated more in the adult novel pattern task [$b = 0.57$, CI 95% = (0.09, 0.97)], ($t_{528} = 2.82$, $p = 0.03$) (**Figure 6**).

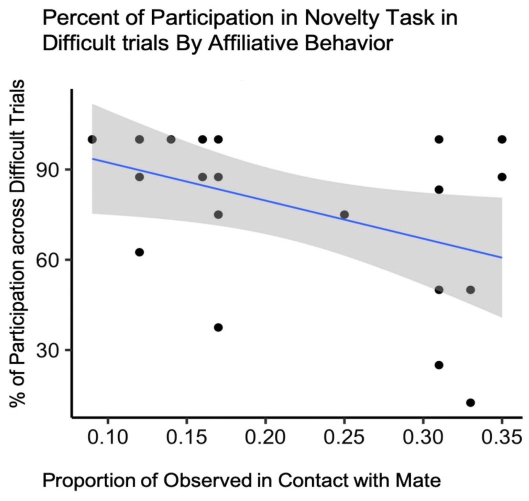

FIGURE 4 | Novelty response task participation (*N* = 11) by Affiliative Contact. Percentage of subject participation across difficult trials plotted against the proportion of time subjects were observed in contact with their mate.

Experiment 2

There were not enough instances of adverse experience that occurred before the 4-month IOF test to examine possible changes in behavior during the test, but previous work in our lab has shown a decrease in the time infants with adverse experience spend in the grate zone during the father condition compared to typically reared infants (Larke et al., 2017). Similar to Experiment 1, infant vocalization, grate touch, and grate zone behavior did not explain significant amounts of variability in adult affiliation and were therefore excluded from the final model.

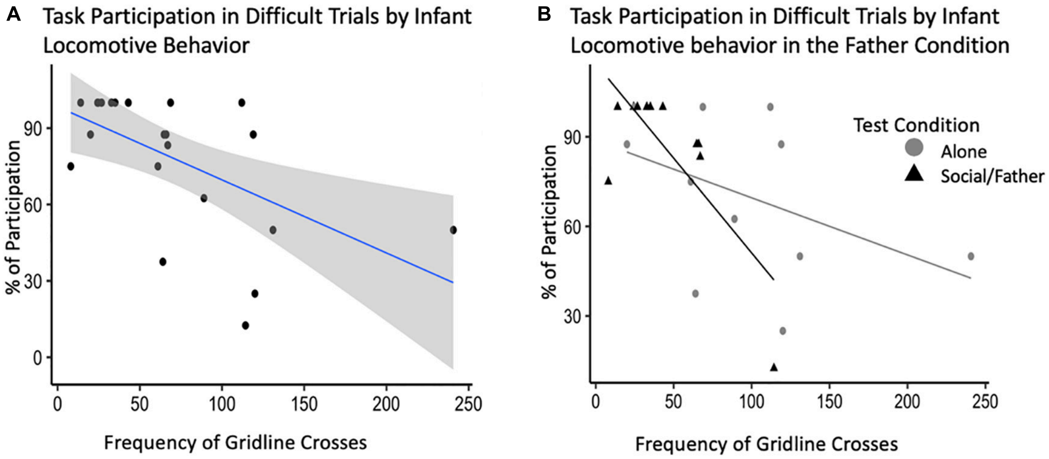

FIGURE 5 | Novelty response task participation (*N* = 11) by infant behavior, specifically, locomotion. **(A)** Percent of task participation during difficult novelty response task trials plotted by infant locomotor behavior demonstrated by the average frequency of gridline crosses in a trial. **(B)** Interaction plot for the effects of test condition on the relationship between infant behavior and task participation.

TABLE 5 | Summary of results for Experiment 1 in mother condition.

Predictor	Outcome	β	SE	*p*
Infant behavior during mother condition with empty condition as the reference	*Novelty response task participation*			
Social condition		39.31	18.92	0.07
Grate touch behavior (mom)		−0.42	0.23	0.09
Grate zone behavior (mom)		**0.44**	**0.18**	**0.04**
Locomotor behavior (mom)		**−0.25**	**0.12**	**0.05**
Social condition * grate touch behavior		**0.57**	**0.20**	**0.03**
Social condition * grate zone behavior		−0.20	0.26	0.47
Social condition * locomotor behavior		−0.24	0.11	0.08

Multiple linear regression model (N = 11) of adult participation in the novelty response task from behavior in the mother infant open field condition. Boldface indicates statistically significant predictors.

With the current data collected on adverse early experience, the difference in locomotor behavior from the father condition to the empty condition, and the interaction between these two independent variables and proportion of observed time spent in proximity or contact with their adult pair mate, we attempted to fit a model of linear growth and observe whether or not this accurately characterized the data compared to the null model. While our model had a lower residual sum of squares than the null, it did not significantly outperform the null model so we report the following findings with caution. Although group comparisons did not reveal a significant difference in adult affiliation by early experience for either contact or proximity behavior (F_{16} = 0.01, p = 0.92; F_{16} = 0.09, p = 0.77, respectively) we did observe some interactions. For adult contact behavior, there was a trend such that infants with a greater change in locomotor behavior between conditions were observed in contact with their mate more often than infants with smaller changes in locomotor behavior, unless the infant experienced adversity during development [standardized β = −1.30, CI 95% = (−1.30, −1.29), p = 0.060] (**Table 6**). We ran the same model for adult proximity and found a stronger relationship between infant locomotor behavior and adult behavior [standardized β = −0.777, CI 95% = (−0.779, −0.776), p = 0.045] (**Figure 7**). To confirm the effect was related to infants' primary attachment figure, we also ran the model comparing locomotor behavior when mom was present to the empty condition and found no trends for either contact [standardized β = −0.13, CI 95% = (−0.14, −0.13), p = 0.85] or proximity [standardized β = −0.496, CI 95% = (−0.499, −0.493), p = 0.48].

DISCUSSION

Experiment 1

The current study examined attachment behavior in coppery titi monkeys as a potential animal model of human attachment. We tested whether infant behavior during an IOF test, modified to resemble the Ainsworth Strange Situation Paradigm, could be used to explain variability in adult participation in a novelty response task depending on whether their pair mate was present or absent. Our results should be interpreted as exploratory until more data can be collected, and we can test our hypothesized models. In concordance with human literature reporting stability in attachment behavior from parent–infant bonds to adult

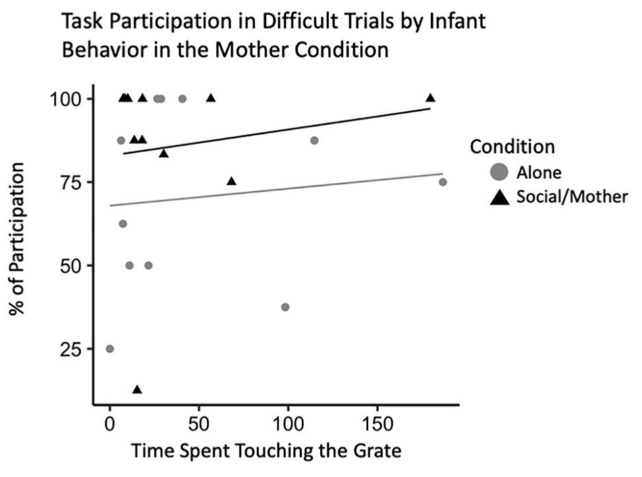

FIGURE 6 | Novelty response task participation (*N* = 11) by infant behavior, specifically, time spent touching the grate. Interaction plot for the effects of test condition on the relationship between infant grate touching behavior and adult task participation during difficult novelty response task trials.

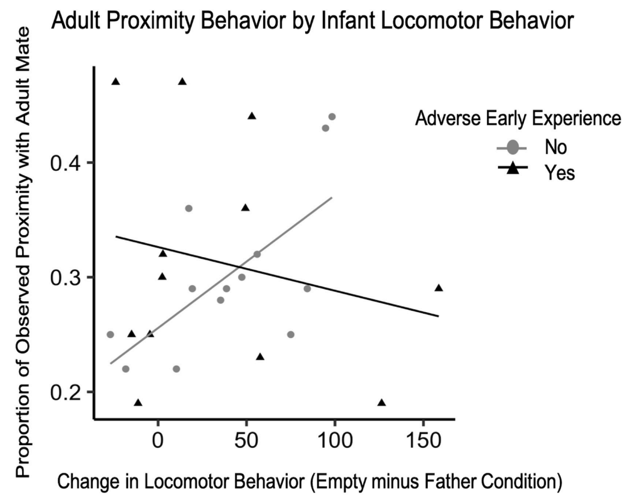

FIGURE 7 | Difference scores for infant locomotor behavior (*N* = 25) plotted against the proportion of observations they were observed in proximity with their mate as adults with lines of best fit.

partner bonds, we found support for our hypothesis that highly reactive infant titi monkeys are also highly reactive as adults within the current dataset (Waters and Merrick, 2000; Fraley, 2002). These subjects exhibited a dramatic change in locomotor, grate touch, grate zone, and vocalization behavior between the alone and father condition in the IOF and a dramatic change in participation rates between the alone and partner conditions during the novelty response task. Our results suggest that the type of attachment behavior which an infant titi monkey displays with their father is indicative of the type of attachment behavior they will share with their adult pair mate. Additional data are needed to test our models and confirm this relationship as predictive rather than correlational.

Although infant vocal behavior, location in the field, and grate touch behavior were not able to explain variability in adult behavior, we found an interesting relationship between infant locomotor behavior in the IOF and adult response to novelty. Considering locomotion as an accepted measure for anxiety-like behavior and the consistency of this behavior with participation in the novelty response task we believe this result is in line with traditional Attachment Theory (Barros and Tomaz, 2002). In the IOF paradigm, nearly all infants locomoted less when they had visual access to their father than when they did not, but the amount that infants locomoted during the father condition varied by individual. Infants with the lowest levels of locomotion in the father condition were the same adults that participated the most in the novelty response task when their pair mate was present. There was no apparent relationship between grate zone behavior when the father was present and adult participation; therefore, we believe this decrease in motor activity was not related to the infant's desire to be in proximity to their father, but rather a more generalized decrease in anxiety-like behavior.

TABLE 6 | Summary of results for Experiment 2.

Predictor	Outcome	β (standardized)	SE	*p*
	Contact with mate			
Adverse early experience		0.06	0.04	0.19
Change in IOF locomotor behavior (father)		0.59	>0.001	0.10
Change in IOF locomotor behavior (mother)		>0.001	>0.001	0.97
Change in IOF locomotor behavior (father) * adverse early experience		−1.30	0.001	0.060*
Change in IOF locomotor behavior (mother) * adverse early experience		−0.18	0.001	0.79
	Proximity to mate			
Adverse early experience		0.42	0.04	0.12
Change in IOF locomotor behavior (father)		0.66	0.001	0.061*
Change in IOF locomotor behavior (mother)		0.45	0.001	0.52
Change in IOF locomotor behavior (father) * adverse early experience		**−0.78**	**0.001**	**0.045**
Change in IOF locomotor behavior (mother) * adverse early experience		−0.50	0.001	0.48

*Linear mixed models (N = 25) of adult affiliative behavior from infant behavior. Boldface indicates statistically significant predictors and * indicates a trend. Adverse early experience was coded as 1 and typical experience was coded as 0.*

Along with Bowlby's initial theory, many studies have pointed out consistencies between infant attachment style and trait outcomes such as anxiety, depression, and the big five personality traits (Hagekull and Bohlin, 2003; Picardi et al., 2005). Although social condition alone was unable to explain task participation, there was an interaction showing that the relationship between infant behavior and adult performance was stronger when the attachment figure was present than when the subject was alone. This suggests that some of our subjects are generally less reactive than others and their ability to cope with strange or novel situations is related to the kind of relationship they have with their attachment figures.

Our results also illustrated a relationship between some infant behaviors and adult participatory behavior when separated from their attachment behavior. When we analyzed infant behavior in the presence of the infant's mother, we found relationships between grate zone behavior and adult participation, as well as an interaction between grate touching behavior and adult participation. We believe these effects are likely due to temperament rather than attachment behavior because we did not observe the same effects for the father condition.

Experiment 1 also explored the relationship between observed affiliation between the subjects and their current pair mate, distress following involuntary separation from their pair mate, and participation in the novelty response task. Although our task elicited the expected anxiety-like response observed in previous studies (Arias del Razo et al., 2019), we were unable to confirm our hypothesis that individuals in pairs exhibiting higher rates of affiliative behavior would be more distressed during a partner's absence, and consequently less likely to participate in the novelty response task. However, our results did show an interesting relationship between affiliative behavior and adult anxiety-like behavior regardless of whether or not their pair mate was present during the task. More affiliative subjects in this dataset were less likely to participate in the task than their less affiliative counterparts. Interestingly, this effect was the opposite for pairs in their second or third pairing but given the small sample size of the current study, the relationship between pair experience, affiliation, and anxiety-like behavior should be further explored. It is also difficult to know if this effect was driven by pair experience or if there is an effect of age on anxiety-like behavior in titi monkeys, given that the subjects with more pair experience were also the oldest in the study. Studies in humans suggest that older individuals report fewer symptoms of generalized anxiety (Byers et al., 2010; Miloyan et al., 2014).

The role of social buffering during an anxiety response is complex. Ditzen et al. (2008) investigated differential psychological and physiological responses to the Trier Social Stress Test in individuals with anxious or avoidant attachment styles according to Attachment Theory. Their findings suggested some interactions between attachment behavior and stress response, but they were inconclusive in terms of whether or not these individuals were specifically responding to the social support differently. Similarly, in our study, we were unable to see a clear change in behavior as a result of the presence or absence of their pair mate, but we did see an interaction between attachment behavior and test condition such that the individuals most calmed by their fathers also tended to receive the most benefit from having their pair mate present. Although the effect of social condition did not stand out in our experiment, we do not believe this to be indicative of a lack of social support from their pair mate.

Adult titi monkeys are more likely to engage with a novel object and exhibit lower levels of autonomic arousal when their pair mate is present (Cubicciotti and Mason, 1975; Fragaszy and Mason, 1978; Hennessy et al., 1995). It is possible that our testing paradigm did not initiate a strong enough reaction to involuntary separation to inhibit behavioral response during testing. However, we believe it is more likely that the lack of statistical evidence of social support in the current study is due the specific individuals in the subject pool. Of our 11 subjects, only 7 of them were engaged in their first adult pair bond while the other 4 were currently paired with their second or even third pair mate. Prior to the design of this experiment, we did not expect titi monkey attachment behavior to change over the course of multiple pair bonds. New data from our lab show a clear increase in affiliative behaviors for males in their second pair bond compared to their first (Witczak et al., in preparation). These new findings indicate the need for further investigation of the flexibility of attachment behavior in adult titi monkeys.

Experiment 2

In Experiment 2, we tested whether infant attachment behavior was directly related to adult affiliative behavior. To our knowledge, this is one of the first studies indicating a change in attachment behavior, as described in Attachment Theory, from infancy to adulthood resulting from adverse life events in NHPs. As we observed in Experiment 1, our results indicated that, of all the infant behaviors we measured, only locomotive behavior was indicative of adult behavior. Until we are able to test this hypothesis on a new data set, we can only interpret these results as they relate to these specific animals, not the entire population. For these titi monkeys, infant locomotion, or anxiety-like behavior, trends with adult proximity behavior during the first 6 months of their first pair bond. There appears to be a negative correlation between the extent to which the infant is "calmed" by their father's presence and their adult proximity seeking behavior. Perhaps more interesting is the significant interaction between this trend and adverse early experience in titi monkeys. For subjects with typical early experience, the less they locomoted when their father was present compared to his absence (i.e., how "calmed" they were by their attachment figure), the more affiliative they were in pairs as adults. However, infants with adverse early experience, but similar locomotor responses during the IOF test, did not follow this pattern. While affiliative behaviors did not differ by group (adverse vs. typical), the developmental trajectory appears to be altered. Our sample size was not sufficient to thoroughly assess whether the interaction was driven by some infants responding to adverse experience by becoming more affiliative or less affiliative, but we can see that their infant attachment behavior is incongruent with their adult attachment behavior. Given that the current study did not control for genetic variability between our adverse and typical groups, we are unable to conclude if the adverse experiences themselves attributed to incongruent attachment behavior or if group differences were due to genetic differences (Barbaro et al., 2017).

Human and NHP research have documented changes in attachment behavior resulting from adverse early experiences or negative life events (Harlow, 1964; Bowlby, 1982; Weinfield et al., 2000). Adverse early experiences related to the caregiver have been shown to alter specific brain regions related to social behavior (Yan et al., 2017). Macaque infants that experienced abusive behavior from their mothers illustrated higher rates of anxiety-like and proximity seeking behavior throughout development (McCormack et al., 2006). It is difficult to tell if a similar effect was occurring in our subjects, but there is evidence in NHPs that adverse experiences during critical developmental periods can have long-term implications for the HPA axis and stress-related behavior (Sanchez et al., 2010; Koch et al., 2014). Unfortunately, none of these studies followed their subjects through development into adulthood to investigate possible effects on social behavior so we do not currently have any insight as to how adverse early experience is affecting titi monkey neurobiology. We believe our findings suggest that titi monkeys could play an integral role in understanding these neurobiological changes specifically related to pair bonding.

Limitations

Despite the benefits of studying titi monkeys in a laboratory setting, the current study had several limitations. Most importantly, investigating attachment behavior can be difficult with a small sample size because of the natural variation in behavior. All of our reported results are exploratory and should be considered as hypothesis-generating rather than confirmatory. In humans, insecure attachments are observationally and biologically very different from secure attachments. For example, infants with some types of attachment insecurity exhibit dramatic increases in proximity seeking behavior while others exhibit decreases. A comprehensive analysis of adult attachment styles in non-clinical European subjects classified 58% of the population as secure and divided the other 42% of subjects into four categories of insecure attachments (Bakermans-Kranenburg and van IJzendoorn, 2009). With a sample size of 25 we were unable to confidently classify our subjects into different categories of attachment and as such we were not able to control for behaviors linked to those individual differences. More research is needed in order to fully understand the variability of attachment behavior in titi monkeys.

CONCLUSION

Although a lot of work has been done in rodents and other NHP models investigating the effects of adverse early experiences on social behavior and health outcomes there is still a great need for direct investigation of the development of adult pair bonds (Rincón-Cortés and Sullivan, 2016; Fraley, 2019; Hennessy et al., 2019). Our current findings lay the groundwork for a NHP model of the attachment system across the life span. As noted in the section "Limitations," our sample size was too small to test our models' predictive ability and future studies will need to address this in order to understand the relationship between infant and adult attachment behavior. We ran power analyses for both Experiment 1 and Experiment 2 and found that future studies would need samples sizes of 50 and 22, respectively, for statistical power of 0.80. Future studies in monogamous NHPs have the potential to precisely identify key periods for the development of the attachment system in a way that has proven very difficult in humans. Identifying these periods will expand our knowledge of how social attachments affect our biology and provide more opportunities to test potential interventions.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the University of California, Davis Institutional Animal Care and Use Committee.

AUTHOR CONTRIBUTIONS

LS collected the data, designed and performed the analyses, and wrote the first draft of the manuscript. KB obtained the funding for the project, participated in the research and analytical design, and edited the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.00025/full#supplementary-material

TABLE S1 | Results from all log-likelihood tests for model comparison.

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Viewing Romantic and Friendship Interactions Activate Prefrontal Regions in Persons With High Openness Personality Trait

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The personality traits we have and the closeness we experience in our relationships inevitably color the lenses through which we perceive social interactions. As such, the varying perceptions of our social relationships could indicate underlying differences in neural processes that occur in the prefrontal cortex (PFC), a brain region involved in social cognition. However, little is known of how personality traits and relationship closeness with others influence brain responses when viewing social interactions between kin (i.e., siblings) and non-kin (i.e., romantic, friends) partners. In the present study, functional near-infrared spectroscopy (fNIRS) was employed to investigate prefrontal cortical activation patterns in response to three 1-min mute video clips depicting a male–female couple interacting with comparably mild levels of affection while baking, exercising, and eating. The context of the interaction was manipulated by informing participants about the type of relationship each couple in the three video clips was in: (a) romantic partners, (b) friends, or (c) siblings. By changing only the contextual labels of the videos, we revealed distinct PFC responses to relationship type as a function of *openness* trait, closeness with romantic partner, and closeness with siblings. As *openness* score increased, we observed an enhanced activation of the left inferior frontal gyrus (IFG), the left anterior PFC (aPFC), and the right frontal eye fields (FEFs) in response to the video labeled *romantic* and *friendship*, but a reduction in these areas in the *siblings* condition. Similarly, individuals with higher romantic and sibling closeness showed increased activation in the IFG and dorsolateral PFC (dlPFC) in response to *romantic* and *friendship* conditions, but decreased activation in the *siblings* condition. Differences in PFC activations toward romantic, friendship, and sibling relationships reflect underlying variations in the cognitive processing of social interactions, depending on the personality (i.e., *openness*) and experiences (i.e., relationship closeness) of the individual, as well as the relationship type with which the interaction is labeled.

Keywords: relationships, openness, personality, fNIRS, prefrontal cortex

INTRODUCTION

Human affiliations are entrenched in interpersonal love, which has been described as a deep sense of close attachment between two people (Berschied and Peplau, 1983). Depending on whom we share it with, this attachment manifests within varying forms of relationships with kin (i.e., siblings) and non-kin (i.e., friends and partners) individuals. Within low fertility social environments, that is, societies with fertility rates that are lower than the replacement rate of 2.1, where individuals have fewer siblings and cousins, human non-kin relationships are becoming increasingly significant in our lives. The amount of social investment that is required for us to maintain kin and non-kin relationships starkly differs. While the former is perceived to be more stable and granted, the latter requires constant monitoring and personal commitment (Stewart-Williams, 2007; Rotkirch et al., 2014).

Perceptions of social interactions are accompanied by distinct responses in the prefrontal cortex (PFC), a brain area that has been established to occupy an integral role in the interpretation of affective information and in performing higher order socio-cognitive functions (Güroğlua et al., 2008; Cacipoppo et al., 2012; De Boer et al., 2012). Within the medial region of the PFC, the dorsomedial PFC (dmPFC) and ventromedial PFC (vmPFC) networks, in particular, contribute significantly to these processes. For instance, passive viewing of video scenes featuring social interactions between characters was sufficient to significantly elicit dmPFC activity (Wagner et al., 2016). Equally important to affective interpretation is the vmPFC, which has been shown to underscore social judgments of an agent's capability of possessing a mind (i.e., mind perception). Wiese et al. (2018) found that when participants engaged in a mind perception task that required them to judge the internal mental states of faces which differed in their resemblance to human faces, activity of the vmPFC was found to be significantly associated with mind perception. Aside from the medial networks, the lateral networks of the PFC are also consistently implicated in the regulation of emotions (Ochsner et al., 2012; Tully et al., 2014). For instance, enhanced activation of the ventrolateral PFC (vlPFC) during social exclusion, a form of social stress, is related to lower self-reported ratings of distress (Eisenberger et al., 2003). Given the extensive involvement of prefrontal areas in socio-cognitive processes, we postulate that the PFC is likely to govern differences in perception of social interactions.

Distinct patterns of PFC activation have been found across relationship types as well. For example, in a study that compared the presence of a romantic partner against that of a friend during emotional regulation in response to threatening stimuli, researchers observed greater activation of the vmPFC region in the presence of the romantic partner (Morriss et al., 2018). Their findings suggest that, even in the absence of social interaction, the relationship category of the co-present individual is associated with unique neural responses in the PFC. In another study, Bartels and Zeki (2004) demonstrated that differences in PFC activity was evident between participants who were shown an image of their romantic partner, compared to those who were presented with an image of their child. Heightened activation of the lateral regions of the PFC was observed only for the group that was exposed to images of their child. Similarly, their findings accentuated the pivotal role of the PFC in processing different relationship types. Given the function of the PFC in processing both social interactions and relationship categories, the present study serves as the first to investigate PFC activities when individuals are presented with scenes of social interactions, of comparatively mild affection, labeled with different relationship types.

Personality is defined as one's characteristic set of thoughts, feelings, and behaviors. There are a number of personality models such as Allport's trait theory, the Big Five model, and the HEXACO model, that have been proposed (see Cervone and Pervin, 2013; Matz et al., 2016). According to the Big Five model, one of the most dominant and widely used frameworks, personality comprises five core dimensions, namely, *Openness to Experiences (i.e., Openness), Conscientiousness, Extraversion, Agreeableness, and Neuroticism,* which are essential in the interpretation of interpersonal experiences (Hines and Saudino, 2008). In a large representative study, Laakasuo et al. (2017) utilized data from an extensive British Household Panel Survey ($N = 12{,}098$) to examine the link between an individual's personality traits and the characteristics of his/her three closest friends. They found that, among the five variables, *openness* was the only trait shown to be correlated to all characteristics of close friends included in the study. For instance, those with higher openness are more likely to have "less traditional friendships," such as having friends from another country, and possess more friends of the opposite gender. Their findings imply that persons with higher openness trait are likely to establish friendship styles that are exploratory in nature. These results generally signify an association between personality and meaningful differences in the characteristics of one's close friends. Laakasuo et al. (2017) suggested that the different associations between personality traits and characteristics of close friends could be an indication of varying strategies in the compilation of social networks across individuals. Taken together, these findings suggest the pertinent role of personality traits, *openness* in particular, in influencing non-kin relationships.

Despite the rich body of knowledge in this field, there is a paucity in the investigation of the influence of personality constructs on prefrontal cortical mechanisms of kin and non-kin relationship perception. Compared to more stable kin relationships, non-kin relationships demand greater social investment and attention (Stewart-Williams, 2007; Rotkirch et al., 2014). Little is understood, however, of how differences in social investment moderate distinct perceptions of social interactions between kin and non-kin pairs. Moreover, since the degree of openness was postulated to govern differences in social networking strategies (Laakasuo et al., 2017), there is a possibility that openness would likewise be associated with distinguishing kin from non-kin interactions. To that end, the present study measured the effect of personality variables on prefrontal cortical responses to scenes of kin (i.e., sibling) and non-kin (i.e., friendship and romantic) interactions. Functional near-infrared spectroscopy (fNIRS) offers a sensitive way to record the often nuanced and subtle differences in prefrontal brain responses.

Participants were exposed to scenes depicting a male–female pair interacting with comparably mild displays of affection while baking, exercising, and eating. While the order of presentation of video stimuli remained the same, the label attached to the video, either *romantic partners*, *siblings*, or *friendship*, differed across participants. Although the primary focus of the study is on the distinction between kin and non-kin relationships, the non-kin category was further subdivided into *romantic partners* or *friendship* to account for the comparatively greater physical intimacy that is typically expected of the former relationship type. We embarked on this experiment with three hypotheses in mind. First, we anticipated a distinction in medial and lateral PFC activity in response to kin (i.e., sibling) and non-kin (i.e., friendship and romantic) relationships as a function of *openness*. Given that our participants are young adults in a contemporary low fertility society who are likely to invest in the maintenance of previously established friendships while pursuing romantic relationships (Arnett, 2004), and that *openness* is the strongest predictor of traits in friendships, it is likely that PFC activation patterns in response to kin and non-kin interactions differ depending on one's level of *openness*. Second, since the intensity of affect among siblings follows a linearly decreasing trend into adulthood, whereas that of friends shows an opposite positive trend (Bradac, 1983), we expect that the activities of medial and lateral PFC would depict an inverse relationship between kin and non-kin interactions as a function of relationship closeness. It would, however, be naïve to assume that all kin and non-kin relationships conform to this common trend. While most young adults may veer toward the company of friends and the pursuit of romantic partners, some may nonetheless find comfort with their existing sibling relationships. To account for such individual differences, a measure of relationship closeness across each of the three relationship types would also be obtained. Thus, our third hypothesis is that PFC responses to kin and non-kin interactions may differ as a function one's closeness level in each relationship type.

MATERIALS AND METHODS

Participants

A total of 44 heterosexual women ($M = 21.2$ years, $SD = 1.66$) and 25 men ($M = 21.4$ years, $SD = 1.61$) were recruited either as paid participants or psychology undergraduates compensated with course credits. The study was approved by the ethics committee and informed consent was obtained from all participants prior to the study. Information regarding participants' demographic data can be found in **Table 1**. A preliminary data analysis was conducted to determine whether there were significant group differences between participants in terms of the types of relationships they had. Welch's t-test analyses were conducted on the openness scores of the following groups of participants: (i) with and without siblings of the opposite gender ($t = 0.311$, $df = 60$, $p = 0.757$); (ii) with and without at least one past romantic partner ($t = -1.912$, $df = 67$, $p = 0.060$); (iii) who are currently in a romantic relationship compared to those who are not ($t = 1.091$, $df = 45$, $p = 0.281$), and (iv) across male and female sex ($t = -0.002$, $df = 67$, $p = 0.998$). Median split followed by t-tests were also conducted on the age of participants (median = 21, $t = -0.147$, $df = 67$, $p = 0.883$) and number of siblings that participants have (median = 1, $t = -0.267$, $df = 67$, $p = 0.790$). As no significant group differences were found, all individuals in the sample were treated as a group accordingly.

TABLE 1 | Participants' demographic information.

Demographics	Frequency
Gender	
Male	25
Female	44
Age (years)	
18	1
19	15
20	7
21	14
22	16
23	10
24	5
25	1
Number of siblings	
0	7
1	34
2	24
3	3
4	1
Siblings of the opposite gender	
Yes	38
No	24
At least one past romantic relationship	
Yes	47
No	22
Currently in romantic relationships	
Yes	26
No	21

Questionnaire

Personality Questionnaire

Participants were required to complete a personality questionnaire prior to attending the experimental session. The Big Five questionnaire is a 50-item self-report questionnaire on a five-point Likert scale, which requires the participant to report how accurate a sentence is (from 1 = very inaccurate to 5 = very accurate) in describing them (John et al., 1991). The Big Five questionnaire consists of five personality dimensions—*Openness* to experience, *Conscientiousness, Extraversion, Agreeableness,* and *Neuroticism* (Digman, 1990). When administered in college settings, internal consistency measures found this questionnaire to be reliable, with Cronbach's α of over 0.70 for each trait (Ward, 2017). In our sample, the Cronbach's α for *Openness* is 0.817.

Personal Relationship Closeness Questionnaire

Given that numerous external variables shaped social relationships, we recognized that across individuals, the perception and experience of a particular relationship would differ regardless of whether the relationship was kin or non-kin in nature. Hence, personal relationship closeness (Personal-RC) was administered to account for individual differences in social relationships as a function of how close they perceive these relationships to be. The Personal-RC questionnaire is adapted from the Relationship Closeness Inventory (RCI) (Berscheid et al., 1989) with regard to the relationships of participants with their romantic partners, friends, and siblings. For the friendship subscale, participants were asked to respond regarding their "closest friend" in the questionnaire as follows: "This section consists of questions regarding you and your friendships. Think of your closest friend while answering the following questions." This inventory consists of one six-point Likert scale item "What is/was/will be the average amount of time you spend with each other per week (in hours)" as well as two five-point Likert scale items "How much influence do you think this person has in your everyday decision-making?" and "How much influence do you think this person has in your important life events?." An open-ended item regarding the duration of acquaintance was also included "How long have you known this person for (in years)?." In our sample, the Cronbach's α for closeness with romantic partner, friends, and siblings are 0.857, 0.772, and 0.865, respectively.

Experimental Design

Participants were seated alone in a dimly lit room and presented with a series of three videos on a 15-inch screen laptop PC, along with a randomized description of the actors' relationship in each video. At the start of the experiment, a fixation cross against a blank screen was shown to the participant for 30 s, before a 15-s instruction page was displayed. A short description of the relationship between the male–female pair, (a) Romantic partners, (b) Friendship, and (c) Siblings, and the activity within the video, (i) baking, (ii) exercising, and (iii) eating, were shown on the screen for 10 s before the onset of the video stimuli. An inter-stimulus interval (ISI) of 30 s preceded the 10-s description of the subsequent video. Likewise, a recovery period of 30 s, followed by a 10-s description, occurred before the onset of the final video (**Figure 1**).

The mute videos were shown in the same order (i ii iii) to all participants but the relational context in which the interaction occurred was manipulated by informing participants of the nature of the relationship. Prior to the experimental session, participants were randomly assigned into three groups, where they were told that the relationship corresponding to the videos were as follows: a b c; b c a; and c a b. This experimental design fixed the order of activity of the videos across all participants (i ii iii), while changing only the description of the relationship type matched to the videos.

Video Stimuli

A digital video recording of the three stimuli was performed using an OPPO video camera. Three different pairs of opposite-gendered actors, of Chinese ethnicity, were recruited to engage in similar levels of mild displays of affection which was filmed in three separate videos. All videos were filmed from the same angle and distance, showing only the two actors and no other persons. In the video, actors interacted with each other in the following social contexts: (i) while baking together, (ii) while exercising together, and (iii) while eating together. The videos were edited to control for visual parameters (i.e., brightness, hue) and all sounds were removed. The duration of each clip was cut to 60 s.

During the experiment, the relational context of each video was manipulated by changing the description of the relationship of the actors given to the participants. We conducted a pilot test of the videos to ensure that this manipulation was valid. Six different videos were filmed and a focus group discussion was held with the participants of the pilot test ($n = 10$) to decide on the videos to be used in the study. We asked participants in the pilot test regarding the (i) plausibility of these activities occurring between individuals in the three types of relationships tested (romantic partners, friends, and siblings) and (ii) extent to which they believed that the actors in each video could be thought of as being either romantic partners, friends, or siblings. The final videos used as the experimental stimuli were those agreed by participants during the focus group discussion to have met the following criteria: (i) activities could occur between individuals in the three types of relationships and (ii) actors could be believed to be either romantic partners, friends, or siblings.

Functional Near-Infrared Spectroscopy (fNIRS) Data Acquisition

As participants viewed the videos, data were recorded using a functional NIRS imaging system (NIRSport, NIRx Medical Technologies LLC, Glen Head, NY, United States) with eight LED-sources and seven detectors, corresponding to a 20-channel montage of the PFC. Dual wavelengths of 760 and 850 nm were used to measure hemodynamic changes in oxygenated (HbO) and deoxygenated (HbR) blood. The signal was recorded at a sample rate of 7.81 Hz on NIRStar Software 14.0.[1] NIRS allows for the monitoring of localized changes in blood oxygenation which serves as a proxy of brain activation. Signal quality was adjusted and calibrated on NIRStar prior to the start of the experiment. The dataverse for this study has been published at: https://doi.org/10.21979/N9/TSVWRR.

NIRS Pre-Processing and Analyses

NIRS data were pre-processed using NIRSLab ver. 2016.[1] Discontinuities were removed, and spikes were identified via visual inspection and replaced with signals nearest to the spike artifacts. Channels with significant noise (gain > 8 and CV > 7.5) were excluded from further pre-processing. A bandpass filter of 0.1–0.2 Hz was applied to eliminate any physiological slow signal and baseline shift variations. Following that, hemodynamic states were measured using a modified Beer–Lambert Law with differential pathlength factor (DPF) of 7.25 and 6.38 for 760 and 850 nm wavelengths, respectively.

Analyses of the pre-processed NIRS data were conducted at two levels: within-subject analysis (first-level) and group-level analysis (second-level). At the first level of analysis, beta-coefficients for each of the relationship conditions were extracted

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[1] https://nirx.net/nirstar-1/

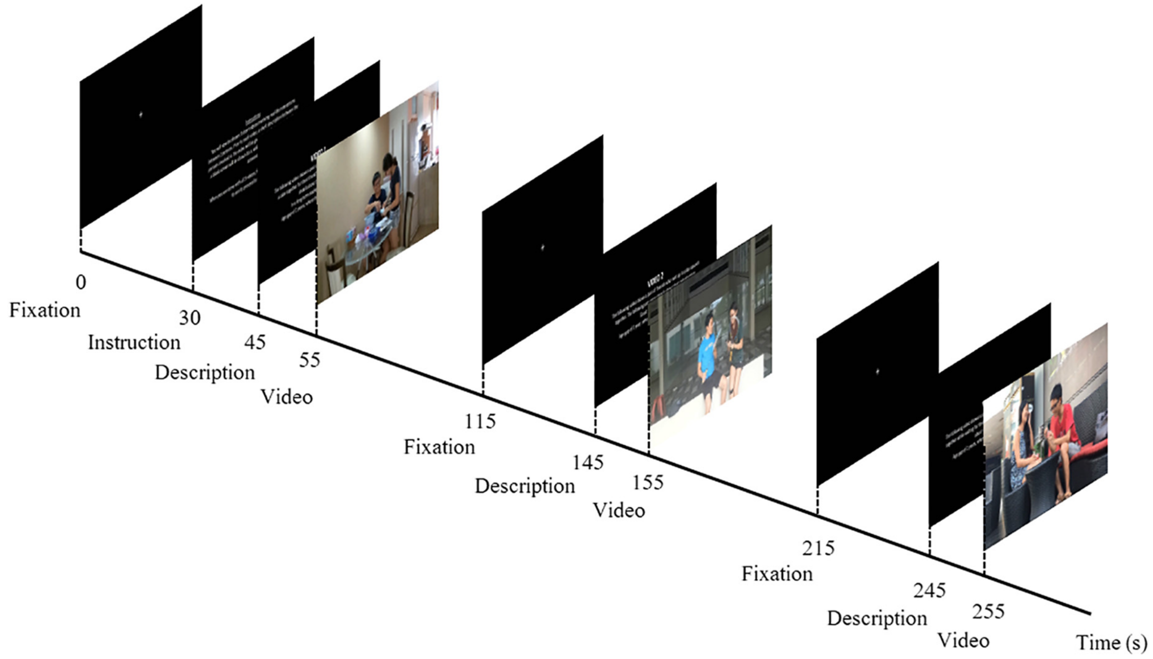

FIGURE 1 | Schematic diagram of experimental design. At the start of the experiment, a fixation cross was displayed against a black screen for 30 s, and this was followed by the instructions for the task, which lasted for 15 s. A description of the first video was screened for 10 s before the onset of the first video stimulus. Each video clip was screened for a duration of 60 s, which was subsequently followed by a recovery period (i.e., fixation cross) of 30 s before the description of the next video was depicted. A total of three video clips were shown, depicting a male–female pair interacting in the following activities: (i) baking, (ii) exercising, and (iii) eating. While the order of activities that the male–female pair engaged in was fixed (i ii iii), the description of the type of relationship corresponding to the video, (a) Romantic, (b) Friendship, and (c) Siblings, was counterbalanced across participants: Romantic–Friends–Siblings (a b c), Friends–Siblings–Romantic (b c a), and Siblings–Romantic–Friend (c a b).

from the GLM of each individual participant. The GLM was based on a hemodynamic response function (HRF) setting and followed a Gaussian full-width at half-maximum (FWHM) 4 model. Discrete cosine transform (DCT) function with a high-pass period cut-off of 128 s was applied to the matrix before the beta-coefficients were obtained.

At the second level of analysis, beta-coefficients from each participant were combined into group-level GLMs. To test the first hypothesis, that *openness* moderates PFC activation differently in response to *romantic partners*, *friends*, and *sibling* conditions, five GLMs were conducted on each channel to investigate the significance of each personality dimension. The dependent variable in each model was the beta-coefficient values, while the independent variable was the relationship condition and participants' personality score (i.e., beta-coefficient ∼ relationship condition * *openness*). GLM analyses were conducted on each of the 20 channels. Since the results were corrected for a large number of multiple comparisons across channels, each personality dimension was tested in a separate GLM to reduce the degrees of freedom in each model. To test the second hypothesis, that an inverse trend of prefrontal responses would be observed for kin and non-kin relationships as a function of *openness*, Pearson's product–moment correlation test would be conducted for channels which emerged to be significant from the GLM analyses.

To test the third hypotheses, that relationship closeness moderates PFC activation differently in response to *romantic partners*, *friends*, and *sibling* conditions, three GLMs were conducted for each channel, where the independent variables were participants' *romantic closeness* (i.e., beta-coefficient ∼ relationship condition * *romantic closeness*), *friendship closeness* (i.e., beta-coefficient ∼ relationship condition * *friendship closeness*), and *siblings closeness* (i.e., beta-coefficient ∼ relationship condition * *siblings closeness*). First, false discovery rate (FDR) correction was applied across 20 channels (Benjamini and Hochberg, 1995) to account for multiple comparisons so as to obtain a corrected *p*-value for each channel. Next, each of these corrected *p*-values were compared against the new critical *p*-value for each channel (p = 0.0167) which was Bonferroni corrected. Only FDR corrected *p*-values that survived Bonferroni correction would be reported as significant. Pearson's product–moment correlation test would also be conducted on significant channels to determine the direction of effect of relationship closeness on PFC activity.

RESULTS

Relationship Type and *Openness*

A generalized linear model (GLM) analysis was conducted on the HbO beta-coefficients (*relationship type* as within-participant factor and *openness* as covariate). Significant *relationship type* and *openness* interaction, which survived multiple comparisons correction, was obtained in the left inferior frontal gyrus [IFG, BA45L—Channel 3, $F_{(2,189)} = 3.117$, corrected $p = 0.0138$, $\eta_p^2 = 0.032$], the left anterior PFC [aPFC, BA10L—Channel 6, $F_{(2,192)} = 6.543$, corrected $p = 0.0138$, $\eta_p^2 = 0.064$], and the right frontal eye field [FEF, BA08R—Channel 10, $F_{(2,162)} = 8.943$, corrected $p = 0.00414$, $\eta_p^2 = 0.099$). No main effects of *relationship type* and *openness* emerged.

Relationship Type and *Openness* Interaction

(a) In the left IFG (BA45L—Channel 3), Pearson's product–moment correlation revealed a negative correlation between *siblings condition* and *openness* (SO; $r = -0.364$, $t = -3.097$, $df = 63$, $p = 0.003$, power = 0.85). The correlations between *romantic condition* and *openness* (RO; $r = 0.067$, $t = 0.531$, $df = 63$, $p = 0.597$, power = 0.082), and *friendship condition* and *openness* (FO; $r = 0.191$, $t = 1.54$, $df = 63$, $p = 0.128$, power = 0.33) were not found to be significant. To evaluate the significance of the difference between two correlation coefficients, a Fisher r-to-z transformation was applied. From this analytical step, only the correlation coefficients between FO and SO was found to be significant ($Z = 3.17$, $p = 0.002$; **Table 2A** and **Figure 2A**). No significant difference was observed between the correlation coefficients of RO and SO, as well as RO and FO.

(b) In the left aPFC (BA10L—Channel 6), Pearson's product–moment correlation revealed a negative correlation between *siblings condition* and *openness* (SO; $r = -0.344$, $t = -2.93$, $df = 64$, $p = 0.005$, power = 0.811), and a positive correlation between *friendship condition* and *openness* (FO; $r = 0.281$, $t = 2.34$, $df = 64$, $p = 0.022$, power = 0.628). Fisher r-to-z transformation was applied, producing a significant difference between the correlation coefficients of FO and SO ($Z = 3.6$, $p = 0.0003$; **Table 2A** and **Figure 2B**). The correlation between *romantic condition* and *openness* (RO; $r = -0.065$, $t = -0.52$, $df = 64$, $p = 0.605$, power = 0.081) was not found to be significant. No significant difference was observed between the correlation coefficients of RO and SO, as well as RO and FO.

(c) In the right FEF (BA08R—Channel 10), Pearson's product–moment correlation revealed a positive correlation between *friendship condition* and *openness* (FO; $r = 0.282$, $t = 2.163$, $df = 54$, $p = 0.035$, power = 0.559), and a negative correlation between *siblings condition* and *openness* (SO; $r = -0.414$, $t = -3.342$, $df = 54$, $p = 0.002$, power = 0.893). Fisher r-to-z transformation was applied, producing a significant difference between the correlation coefficients of FO and SO ($Z = 3.72$, $p = 0.0002$), as well as RO and SO ($Z = 3.14$, $p = 0.002$; **Table 2A** and **Figure 2C**). The correlation between *romantic condition* and *openness* (RO; $r = 0.173$, $t = 1.29$, $df = 54$, $p = 0.201$, power = 0.247) was not significant. No significant difference was observed between the correlation coefficients of RO and FO.

No main effect of *relationship type,* and no main effect of the other four personality variables (i.e., *conscientiousness, extraversion, agreeableness, neuroticism*), or their two-way interaction, emerged.

Relationship Type and *Romantic Closeness*

Similarly, a GLM analysis was conducted on the HbO beta–coefficients (*relationship type* as within-participant factor and *romantic closeness* as covariate). Significant *relationship type* and *romantic closeness* interaction, which survived correction, was obtained in the left IFG [BA45L—Channel 3, $F_{(2,189)} = 8.099$, corrected $p = 0.0082$, $\eta_p^2 = 0.079$] and the right lateral dorsolateral PFC [dlPFC, BA09R—Channel 15, $F_{(2,105)} = 7.610$, corrected $p = 0.0082$, $\eta_p^2 = 0.127$]. No main effects of *relationship type* and *romantic closeness* emerged.

Relationship Type and *Romantic Closeness* Interaction

(a) In the left IFG (BA45L—Channel 3), Pearson's product–moment correlation revealed a negative correlation between *siblings condition* and *romantic closeness* (SR; $r = -0.445$, $t = -3.941$, $df = 63$, $p = 0.0002$, power = 0.964). The correlations between *romantic condition* and *romantic closeness* (RR; $r = 0.163$, $t = 1.315$, $df = 63$, $p = 0.193$, power = 0.254), and between *friendship condition* and *romantic closeness* (FR; $r = 0.12$, $t = 0.959$, $df = 63$, $p = 0.341$, power = 0.157) were not significant. Fisher r-to-z transformation revealed significant differences between the correlation coefficients of RR and SR ($Z = 3.55$, $p = 0.0004$) as well as FR and SR ($Z = 3.31$, $p = 0.001$; **Table 2B** and **Figure 3A**). No significant difference was observed between the correlation coefficients of RR and FR.

(b) In the right lateral dlPFC (BA09R—Channel 15), Pearson's product–moment correlation revealed a negative correlation between *siblings condition* and *romantic closeness* (SR; $r = -0.534$, $t = -3.746$, $df = 35$, $p = 0.001$, power = 0.935). Correlations between *romantic condition* and *romantic closeness* (RR; $r = 0.118$, $t = 0.7$, $df = 35$, $p = 0.489$, power = 0.105], and between *friendship condition* and *romantic closeness* (FR; $r = 0.244$, $t = 1.485$, $df = 35$, $p = 0.147$, power = 0.303) were not significant. Applying the Fisher r-to-z transformation, we found a significant difference between the coefficients of RR and SR ($Z = 2.9$, $p = 0.004$) as well as FR and SR ($Z = 3.43$, $p = 0.001$; **Table 2B** and **Figure 3B**).

Relationship Type and *Sibling Closeness*

A GLM analysis was conducted on the HbO beta–coefficients (*relationship type* as within-participant factor and *sibling closeness* as covariate). Significant *relationship type* and *sibling closeness* interaction was obtained in the left middle frontal gyrus [MFG, BA46L—Channel 1, $F_{(2,177)} = 7.626$, corrected $p = 0.01332$, $\eta_p^2 = 0.079$]. No main effects of *relationship type* and *sibling closeness* emerged.

Relationship Type and *Sibling Closeness* Interaction

(a) In the left MFG (BA46L—Channel 1), Pearson's product–moment correlation revealed a negative correlation between *siblings condition* and *romantic closeness* (SR; $r = -0.471$, $t = -4.097$, $df = 59$, $p = 0.0001$, power = 0.973). Correlations between *romantic condition* and *sibling closeness* (RS; $r = 0.164$, $t = 1.276$, $df = 59$, $p = 0.207$, power = 0.242) and between *friendship condition* and *romantic closeness* (FS; $r = 0.123$, $t = 0.998$, $df = 59$, $p = 0.322$, power = 0.166) were not significant.

TABLE 2 | Table depicting significant channels, associated brain areas, *r*-values of correlations, and *Z*- and *p*-values of Fisher's test of difference between two correlation coefficients. **(A)** Correlation between Relationship condition (*romantic, friendship, siblings*) and *Openness*, **(B)** Correlation between Relationship condition (*romantic, friendship, siblings*) and *Romantic Closeness*, and **(C)** Correlation between Relationship condition (*romantic, friendship, siblings*) and *Siblings Closeness*.

(A)

Brain region		***r***			***Z***			***p***		
Channel	**Corresponding area**	***Romantic*-Openness (RO)**	***Friendship*-Openness (FO)**	***Siblings*-Openness (SO)**	**RO-FO**	**RO-SO**	**FO-SO**	**RO-FO**	**RO-SO**	**FO-SO**
CH3	Left inferior frontal gyrus (IFG)	0.067	0.191	**−0.366****	−0.7	2.47	3.17	0.4839	0.0135	**0.0015****
CH6	Left anterior prefrontal cortex (aPFC)	−0.065	**0.281***	**−0.344****	−1.97	1.63	3.6	0.0488	0.1031	**0.0003*****
CH10	Right frontal eye field (FEF)	0.173	**0.282***	**−0.414****	−0.59	3.14	3.72	0.5552	**0.0017****	**0.0002*****

(B)

Brain region		***r***			***Z***			***p***		
Channel	**Corresponding area**	***Romantic*-Romantic Closeness (RR)**	***Friendship*-Romantic Closeness (FR)**	***Siblings*-Romantic Closeness (SR)**	**RR-FR**	**RR-SR**	**FR-SR**	**RR-FR**	**RR-SR**	**FR-SR**
CH3	Left inferior frontal gyrus (IFG)	0.163	0.120	**−0.445*****	0.24	3.55	3.31	0.8103	**0.0004*****	**0.0009*****
CH15	Right lateral dorsolateral prefrontal cortex (DLPFC)	0.117	0.243	**−0.535*****	−0.53	2.9	3.43	0.5961	**0.0037****	**0.0006*****

(C)

Brain region		***r***			***Z***			***p***		
Channel	**Corresponding area**	***Romantic*-Sibling Closeness (RS)**	***Friendship*-Sibling Closeness (FS)**	***Siblings*-Sibling Closeness (SS)**	**RS-FS**	**RS-SS**	**FS-SS**	**RS-FS**	**RS-SS**	**FS-SS**
CH1	Left middle frontal gyrus (MFG)	0.164	0.129	**−0.471*****	0.19	3.61	3.42	0.8493	**0.0003*****	**0.0006*****

**p* < 0.05, ***p* < 0.01, ****p* < 0.001.

Applying Fisher r-to-z transformation, we found a significant difference between the coefficients of RS and SS (Z = 3.61, p = 0.0003) as well as FS and SS (Z = 3.42, p = 0.0006; **Table 2C** and **Figure 3C**). No significant difference was observed between the correlation coefficients of RS and FS.

Relationship Type and *Friendship Closeness*

A GLM analysis was conducted on the HbO beta–coefficients (*relationship type* as within-participant factor and *friendship closeness* as covariate). No significant main effect of *relationship type* or *friendship closeness*, or their two-way interaction was found.

DISCUSSION

The principal aim of this study was to investigate the difference in PFC activation when participants viewed social interactions between male–female kin and non-kin pairs, as a function of personality traits and relationship closeness. The first hypothesis, that variation in level of *openness* will govern distinct medial and lateral PFC activities in response to non-kin (i.e., friendship and romantic) and kin (i.e., sibling) interactions, was fulfilled. The second hypothesis was also satisfied as we found an inverse pattern of cerebral activation that emerged in the left IFG (BA45), left aPFC (BA10), and right FEF (BA8) when viewing *friendship* and *romantic* interactions (i.e., non-kin) compared to *sibling* (i.e., kin) interactions, depending on the *openness* level of the participant. Individuals with higher *openness* trait showed significantly greater activation toward *romantic* than *siblings* condition in the IFG and aPFC. Additionally, those with a higher level of *openness* also exhibited significantly greater activation toward *romantic* and *friendship* conditions compared to the *siblings* condition in the FEF. While the IFG and aPFC fall within the dmPFC and vmPFC networks, respectively, the FEF is located within the ventrolateral network (vlPFC). No other personality trait was found to be significantly related to brain responses when viewing scenes of different relationship categories.

The third hypothesis, that relationship closeness will lead to distinct medial and lateral PFC activation patterns in response to non-kin and kin interactions, was also fulfilled. Similarly, an inverse pattern emerged in response to non-kin (i.e., romantic, friendly) and kin (i.e., sibling) interactions as a

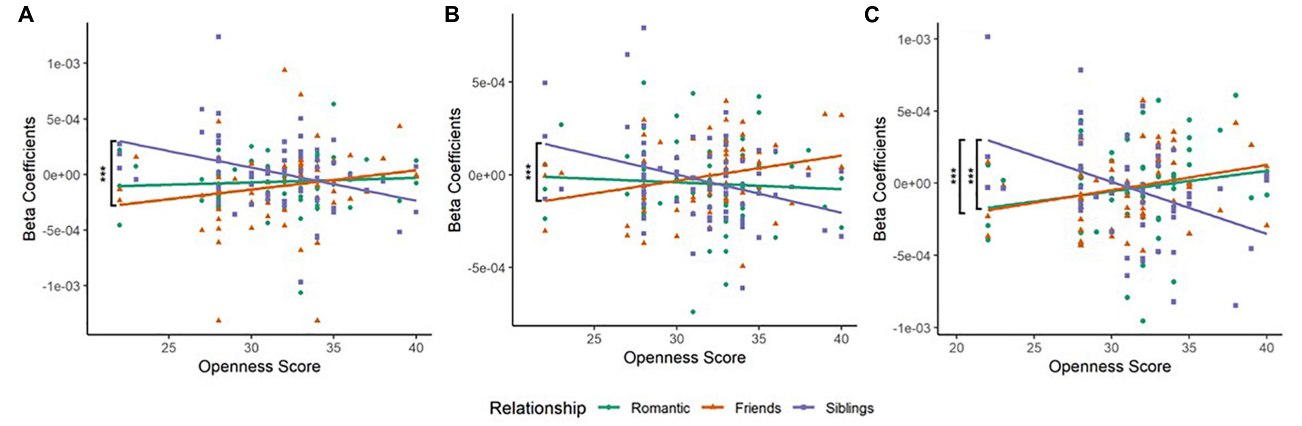

FIGURE 2 | (A) Scatterplot of Relationship type and Openness score in the left inferior frontal gyrus (BA45L—Channel 3). Pearson's product–moment correlations were conducted for each relationship type with openness score: *Romantic*–Openness (RO), *Friendship*–Openness (FO), and *Sibling*–Openness (SO). The difference in correlation coefficients between FO and SO was significant ($Z = 3.17$, $p = 0.0015$). This was observed in the left inferior frontal cortex (IFC). **(B)** Scatterplot of Relationship type and Openness score in left anterior Prefrontal Cortex (BA10L—Channel 6). Pearson's product–moment correlations were conducted for each relationship type with openness score. The difference in correlation coefficients between FO and SO was significant ($Z = 3.6$, $p = 0.0003$). This was observed in the left anterior prefrontal cortex. **(C)** Scatterplot of Relationship type and Openness score in the right frontal eye field (BA08R—Channel 10). Pearson's product–moment correlations were conducted for each relationship type with openness score. The difference in correlation coefficients between FO and SO ($Z = 3.72$, $p = 0.0002$), and RO and SO ($Z = 3.14$, $p = 0.0017$) were significant. This was observed in the right frontal eye fields. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

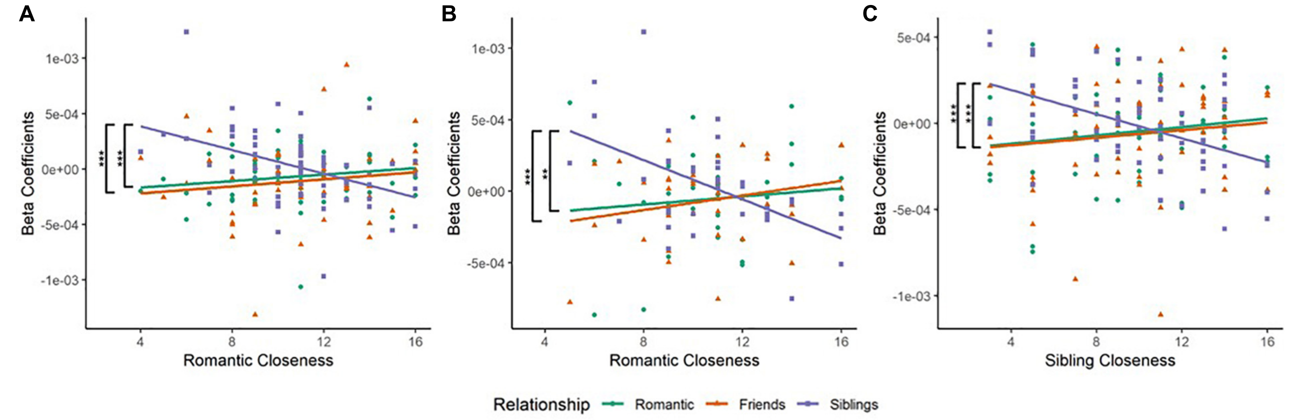

FIGURE 3 | (A) Scatterplot of Relationship type and Romantic Closeness score in the left Inferior Frontal Gyrus (BA45L—Channel 3). Pearson's product–moment correlations were conducted for each relationship type with openness score: *Romantic*–Romantic Closeness (RR), *Friendship*–Romantic Closeness (FR), and *Sibling*–Romantic Closeness (SR). The difference in correlation coefficients between RR and SR was significant ($Z = 3.55$, $p = 0.0004$). The difference in correlation coefficients between FR and SR was also significant ($Z = 3.31$, $p = 0.0009$). These observations were mapped to the left inferior frontal gyrus (IFG). **(B)** Scatterplot of Relationship type and Romantic Closeness score in the right Lateral Dorsolateral PFC (BA09R—Channel 15). Pearson's product–moment correlations were conducted for each relationship type with openness score. The difference in correlation coefficients between RR and SR was significant ($Z = 2.9$, $p = 0.0037$). The difference in correlation coefficients between FR and SR was also significant ($Z = 3.43$, $p = 0.0006$). These observations corresponded to the right lateral dorsolateral prefrontal cortex (DLPFC). **(C)** Scatterplot of Relationship type and Sibling Closeness score in the left middle frontal gyrus (MFG, BA46L—Channel 1). Pearson's product–moment correlations were conducted for each relationship type with openness score: *Romantic*–Sibling Closeness (RS), *Friendship*–Sibling Closeness (FS), and *Sibling*–Sibling Closeness (SS). The difference in correlation coefficients between RS and SS was significant ($Z = 3.61$, $p = 0.0003$). The difference in correlation coefficients between FS and SS was also significant ($Z = 3.42$, $p = 0.0006$). These results were mapped to the left MFG. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

function of *romantic closeness* and *sibling closeness*. We found that individuals with higher *romantic closeness* showed greater activation in the left IFG, part of the dorsomedial network, and the right dlPFC, toward *romantic* and *friendship* condition compared to the *siblings* condition. Moreover, those with higher *sibling closeness* exhibited greater activation in the left MFG, part of the dlPFC network, in response to *romantic* and *friendship* conditions compared to the *siblings* condition. No significant effect of *friendship closeness* was found.

Openness and the Social Brain

Among all other personality dimensions, *openness* most potently governs the development of friendships, where the ideal friend is described to have the same level of *openness* as the individual

(Cheng et al., 1995). As individuals enter adolescence and young adulthood, mild displays of affection among siblings also occur less frequently (Bradac, 1983; Pulakos, 1989). This pattern of socialization is particularly observed in contemporary low fertility societies where emerging adulthood connotes that one consistently interacts with non-kin relations such as friends, rather than kin relations such as siblings, on a daily basis. These findings were later corroborated in a recent study by Laakasuo et al. (2017) who revealed that *openness*, rather than other personality traits, predicted all characteristics of a young adult's closest friends.

Given the pertinent role of *openness* in the development of non-kin relationships, our finding that the level of *openness* is associated with an inverse activation pattern of the IFG and aPFC toward friendly compared to sibling interactions offers a remarkable insight into the mechanisms by which *openness* influences relationship perception. The IFG and aPFC are both located within the larger dmPFC and vmPFC networks, which are known to be recruited for interpretation of social interactions and higher order social cognition, such as making perceptual judgments regarding the mental states of others (Iacoboni et al., 2005; Cleeremans et al., 2007; Schulte-Rüther et al., 2007). Greater activation of the medial PFC in individuals with higher levels of *openness* suggests that they recruited more cognitive resources for affective interpretation of mental states of actors when they were labeled as friends compared to when they were labeled as siblings. It may be possible that persons higher on *openness*, who are prototypically used to having less "traditional" friendships and possess a variety of friends, including more friends from the opposite gender (Selfhout et al., 2010; Laakasuo et al., 2017), engaged in more flexible perceptual assessments when viewing non-kin interactions which was reflected in the brain as greater activation of the medial PFC.

Compared to the medial regions of the PFC, which only distinguished between *friendship* and *siblings* conditions, the ventrolateral region of the PFC, in which the FEF is located, showed an inverse association between both categories of non-kin relationships (i.e., *romantic, friendly*) and kin relationship (i.e., *siblings*). The vlPFC is primarily involved in emotional regulatory processes (e.g., Ochsner et al., 2012). Thus, the distinct pattern of activation in response to non-kin and kin relations that emerged here potentially signals differences in regulatory mechanisms of individuals with higher compared to lower levels of *openness*. Kin and non-kin relations differ fundamentally in the extent of psychological maintenance required of them. While kin interactions are more instrumental and robust, non-kin interactions typically provide greater emotional support despite degrading quickly in the absence of constant social investment (Park and Ackerman, 2011; Roberts and Dunbar, 2011). Compared to their counterparts who scored lower on *openness,* individuals with higher *openness* tend to establish warmer relationships with their siblings (Walęcka-Matyja, 2018). Having safeguarded their "default" kin relationships, individuals with higher *openness* might afford to invest in "chosen" non-kin relationships. Due to their stable kin relationships that demand less social maintenance, more *open* individuals could have required greater emotional regulation only when viewing affectionate interactions between non-kin dyads, whereas less regulatory resources could have been recruited in response to the *sibling* condition.

Relationship Closeness and the Social Brain

With a higher level of *romantic closeness*, greater activation in the *romantic* and *friendship* conditions was observed in the left IFG, situated within the dmPFC, and the right dlPFC. These dorsal regions are implicated in the processing of contextualized social information (Carr et al., 2003; Shamay-Tsoory et al., 2009; Keysers et al., 2010; Schurz et al., 2014) and higher order social cognition, including social perspective-taking and inferring the intentions of others (Miller and Cummings, 2007). In the *romantic* condition, it is likely that greater closeness with romantic partners led participants to enhance the recruitment of these regions for processing of social information in a romantic context. Interestingly, this elevated pattern of activity emerged in the friendship condition as well. Drawing upon kin theories, one postulation is that individuals who are in love are likely to attend to stimuli that encapsulate potential threats in mating, such as the affection shown between non-kin friends of opposite genders. Alternatively, greater activation in the *friendship* condition might simply indicate that processing of social interaction in the context of friendship may be influenced by one's romantic experiences.

An enhanced activation of the dlPFC in both *romantic* and *friendship* conditions might also allude to the possibility that more cognitive resources were required to distinguish between the two complex overlapping relationship types (Backman and Secord, 1959; Sprecher, 1998). Intriguingly, an inverse association was observed in the *siblings* condition, in which a higher level of *romantic closeness* was associated with reduced activation in the dmPFC and dlPFC. This suggests that *romantic closeness* configures an important basis upon which social perceptions of friendship and romantic interactions are formed, both of which are distinct from sibling interactions. Lastly, compared to the *siblings* condition, an unambiguous pattern of similarity between friendship and romantic conditions emerged as a function of *siblings closeness* too. These consistent findings lend support to the notion that kin and non-kin interactions are processed differently in the prefrontal region of the brain.

Future Directions

Although personality represents the main focus of this study, experiential factors in each of these three relationships were investigated by analyzing *relationship closeness*. Comparing *openness* and *relationship closeness*, both analyses revealed a similar negative trend in the *siblings condition,* where higher closeness and openness scores were associated with reduced activation. Moreover, the generally positive correlation between *closeness* and *friendship condition,* and *closeness* and *romantic condition,* paralleled the trend seen as a function of *openness*. This observation brings to bear the question on how personality and past experiences dually operate to elicit a similar influence on the neural events that underscore differential perceptions of relationships. One possible postulation is that there exists an intrinsic link between openness and relationship closeness. Indeed, persons who are more open tend to experience less discord with others, which aids in attaining greater intimacy and closeness in their relationships (Berry et al., 2000). Further studies are required to fully explicate the dynamic effects of personality and experiences on the perceptions of relational interactions.

Limitations and Conclusion

We have revealed the rich influence of the personality trait *openness* in influencing PFC responses to stimuli of different relationship conditions. However, several limitations of this study should be addressed. First, given the methodical limitation of the NIRS device, this study only focused on the prefrontal areas of the brain and marked differences may indeed exist in other cortical or subcortical areas of the brain. Second, subjective behavioral responses of participant ratings on interpersonal parameters of the couples in the videos, such as level of warmth, likeability, affection, and reciprocity were not recorded. A reported enquiry on these dimensions would have further aided the interpretation of the results. Third, control conditions could have been incorporated into the paradigm, such as depicting videos without any actors at all but relaying the same content. Addressing this limitation would have lent greater support to the discriminative validity of the study.

Nonetheless, this study has begun to unearth the neural mechanisms behind how *openness* modulates perceptions of interpersonal interaction (McCrae, 1996; McCrae and Sutin, 2009; Woo et al., 2014). By changing only the labels (i.e., relationship type) of the videos that participants were viewing, we found distinct activation patterns in the IFG, aPFC, and FEF as a function of one's level of *openness*. As *openness* score increased, it was accompanied by elevated activation in these brain areas in response to videos in the *friendship* and *romantic* conditions, but decreased activation when viewing videos in the *siblings* condition. By distinguishing this pattern of response, we have identified the role of *openness* in modulating neurophysiological responses when perceiving social interactions belonging to different relationship categories. This places *openness* at the fore as an integral personality variable that not only dictates how we perceive social relationships, but possibly influences how we exhibit our affections and in turn interpret the affections we receive from different people in our lives. This fascinating finding sheds but a glimmer of understanding on how personality influences the ways in which people comprehend their social world, and how these perceptions take form on a neural level.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found here: doi: 10.21979/N9/TSVWRR.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Nanyang Technological University, Psychology Program, Ethics Committee. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

GE planned and supervised the entire study. AA, PR, PT, and MN collected the data and performed analyses. All authors wrote and commented on the manuscript.

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After the Honeymoon: Neural and Genetic Correlates of Romantic Love in Newlywed Marriages

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In Western culture, romantic love is commonly a basis for marriage. Although it is associated with relationship satisfaction, stability, and individual well-being, many couples experience declines in romantic love. In newlyweds, specifically, changes in love predict marital outcomes. However, the biological mechanisms underlying the critical transition to marriage are unknown. Thus, for the first time, we explored the neural and genetic correlates of romantic love in newlyweds. Nineteen first-time newlyweds were scanned (with functional MRI) while viewing face images of the partner versus a familiar acquaintance, around the time of the wedding (T1) and 1 year after (T2). They also provided saliva samples for genetic analysis (*AVPR1a* rs3, *OXTR* rs53576, *COMT* rs4680, and *DRD4*-7R), and completed self-report measures of relationship quality including the Eros (romantic love) scale. We hypothesized that romantic love is a developed form of the mammalian drive to find, and keep, preferred mates; and that its maintenance is orchestrated by the brain's reward system. Results showed that, at both time points, romantic love maintenance (Eros difference score: T2-T1) was associated with activation of the dopamine-rich substantia nigra in response to face images of the partner. Interactions with vasopressin, oxytocin, and dopamine genes implicated in pair-bonding (*AVPR1a* rs3, *OXTR* rs53576, *COMT* rs4680, and *DRD4*-7R) also conferred strong activation in the dopamine-rich ventral tegmental area at both time points. Consistent with work highlighting the role of sexual intimacy in relationships, romantic love maintenance showed correlations in the paracentral lobule (genital region) and cortical areas involved in sensory and cognitive processing (occipital, angular gyrus, insular cortex). These findings suggest that romantic love, and its maintenance, are orchestrated by dopamine-, vasopressin- and oxytocin-rich brain regions, as seen in humans and other monogamous animals. We also provide genetic evidence of polymorphisms associated with oxytocin, vasopressin and dopamine function that affect the propensity to sustain romantic love in early stage marriages. We conclude that romantic love maintenance is part of a broad mammalian strategy for reproduction and long-term attachment that is influenced by basic reward circuitry, complex cognitive processes, and genetic factors.

Keywords: fMRI, marriage, dopamine, romantic love, pair-bonds

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INTRODUCTION

Pair-bonds appear in nearly all human societies (Schacht and Kramer, 2019), and across other mammalian species (Walum and Young, 2018). Monogamous pair-bonds are characterized by selective partner preference, cohabitation, bi-parental care of offspring, aggression toward strangers, and coordinated behaviors between the couple (Getz et al., 1981; Mendoza and Mason, 1986; de Waal and Gavrilets, 2013; Lukas and Clutton-Brock, 2013). Pair-bonds are thought to have evolved to increase the survival and success of offspring (Walum and Young, 2018). In recent decades ideas about their function have expanded to include companionship, care, and evolutionary fitness (de Waal, 2008; Batson, 2011; Raghanti et al., 2018).

In Western culture, romantic love—defined as a drive for union with a specific other that involves excitement, engagement, and sexual desire (Berscheid and Hatfield, 1969; Acevedo and Aron, 2009)—is closely intertwined with marriage. Romantic love is associated with relationship satisfaction and stability, and individuals' health and well-being. However, for many couples it fades over time (Hatfield et al., 2008). Declines in romantic love often signal trouble for couples, as they are correlated with marital dissatisfaction, increased attention to alternative partners, extra-marital affairs, and divorce (Huston and Houts, 1998; Miller et al., 2006; Maner et al., 2009; Nowak et al., 2014). In addition, relationship problems are non-trivially associated with higher rates of mental and physical health problems, suicide, and homicide (Levenson et al., 1993). Thus, it is important to understand what may help couples to sustain romantic love to ensure the success of marriages and the family unit.

The newlywed years are a critical time that predict long-term marital outcomes (Miller et al., 2006). Specifically, researchers have described "honeymoon effects" in which initially positive and romantic marriages turn sour over time, with sharp declines in love, affection, and positive affect (McNulty et al., 2013; Lorber et al., 2015). Several explanations have been offered for declines in love, from cognitively and perceptually focused "disillusionment" models (Huston et al., 2001; van Dijk and Zeelenberg, 2002; Niehuis et al., 2011, 2018), to affectively focused models centering on increases in stress, negative emotions, and conflict (Bradbury, 1998; Gottman et al., 1998). Yet other models have suggested that habituation, the flattening out of intimacy, diminished sexual frequency, and decreased positive emotions are culprits of honeymoon effects (Baumeister and Bratslavsky, 1999; Jacobs Bao and Lyubomirsky, 2013; Birnbaum et al., 2017; Galak and Redden, 2018).

However, there is some evidence suggesting that marriages may be resilient to the corrosive effects of time. For example, one study showed that in a sample of 1,998 adults examined longitudinally, approximately 40% reported high levels of marital happiness over 20 years (Kamp Dush et al., 2008). Additionally, the happily married group was the most resilient, showing the smallest decreases in life happiness over time. Correspondingly, population studies have shown that approximately 30–40% of individuals in the US married 10 years or more reported high levels of romantic love for their spouse (Acevedo and Aron, 2009; O'Leary et al., 2012). Yet another study demonstrated that couples who idealized each other in the early stages of their relationships were less likely to report steep decreases in love for their partners, measured up to 13 years later (Miller et al., 2006).

To further understand the phenomenon of romantic love maintenance, our overall hypothesis was that romantic love is a developed form of a mammalian drive to find, *and preserve*, preferred mates. Evolution may have selected for diverse strategies in human pair-bonding (some short-term, others long-term) to optimize the chances of offspring survival (Cornwell et al., 2006; Del Giudice et al., 2015; Lim et al., 2015). Our view is consistent with the proposal that love is a complex suite of adaptations that have evolved through sexual reproduction and have, incidentally, turned out to be beneficial beyond mating and bi-parental care of offspring (Buss, 2018). For example, attachment, social bonding, and more generally prosocial behaviors, are thought to have contributed to the advancement of our ancestors through care and cooperation (Baumeister and Leary, 1995).

Thus, we focused on physiological data and studies of non-human mammals as a basis to identify some of the neural and genetic mechanisms involved in sustained romantic love. For example, in monogamous voles the neuropeptides oxytocin (OT) and vasopressin (AVP), and the neurotransmitter dopamine facilitate pair-bonding (e.g., Young et al., 2011). OT and AVP gene polymorphisms, and their receptor-rich brain regions (which are implicated in monogamous pair-bonding), are involved in sexual satisfaction and altruism toward a marriage partner (Acevedo et al., 2019a,b). Moreover, neuroimaging studies by our team, and others, suggest that the mesolimbic reward system is critical for early-stage and long-term romantic love, as well as marital satisfaction (Bartels and Zeki, 2000; Aron et al., 2005; Ortigue et al., 2007; Acevedo et al., 2011, 2012; Xu et al., 2011). Here, we investigated whether these same dopamine-rich reward regions are also involved in the maintenance of romantic love in new marriages.

Several studies have identified genetic polymorphisms associated with pair-bonding. One key polymorphism, *AVPR1a* rs3, has been linked with pair-bonding in voles and humans (Insel et al., 1994; Lim and Young, 2004; Lim et al., 2004; Walum et al., 2008; Jarcho et al., 2011; Acevedo et al., 2019a). In a study of 552 twin pairs and their romantic partners, *AVPR1a* rs3 in men (but not women) was associated with higher levels of partner bonding, fewer relationship problems, greater commitment, and higher levels of relationship quality reported by their romantic partners (Walum et al., 2008). Another study showed that *AVPR1a* rs3 was associated with greater sexual satisfaction and frequency of sexual activity, with corresponding reward system activation in pair-bonded individuals (Acevedo et al., 2019a). More broadly, *AVPR1a* rs3 plays a role in complex social behaviors such as altruism, cognitive empathy, and emotional responsivity to faces (Knafo et al., 2008; Meyer-Lindenberg, 2008; Poulin et al., 2012; Brunnlieb et al., 2016). Thus, we examined the role of *AVPR1a* rs3 in romantic love maintenance.

OXTR rs53576, also identified for its role in pair-bonding behaviors (Poulin et al., 2012; Li et al., 2015; Acevedo et al., 2019b), is a single-nucleotide polymorphism (SNP) of the *OXTR* gene that results in individuals having zero, one, or two G-alleles (versus A-alleles). A greater number of G-alleles is associated with more sociality, empathy (Rodrigues et al., 2009; Buffone and Poulin, 2014; Li et al., 2015; Uzefovsky et al., 2015; Gong et al., 2017), and greater altruism toward a partner (Acevedo et al., 2019b). Additionally, the hormone OT is involved in pair-bonding behaviors such as partner hugs, parenting, orgasm, and partner attractiveness ratings (Grewen et al., 2005; Light et al., 2005; Borrow and Cameron, 2011; Striepens et al., 2011; Scheele et al., 2013). Thus, this was another gene polymorphism that we investigated for its role in romantic love maintenance among newlywed pair-bonds.

The dopamine receptor *DRD4*-7R gene variant is associated with novelty-seeking (He et al., 2018, meta-analysis; Munafo et al., 2008, meta-analysis), sexual behaviors such as a desire to have children earlier in life (Eisenberg et al., 2007), desire for a wider variety of sexual behaviors (Halley et al., 2016), higher rates of promiscuous behavior, and infidelity (Garcia et al., 2010). The *DRD4*-7R genetic polymorphism results in reduced binding for dopamine (Asghari et al., 1995), and thus some have speculated that individuals with this genetic variant generally feel less stimulated and crave novelty (He et al., 2018). Although our examination of *DRD4*-7R was exploratory, prior research studies suggest that this genetic variant is implicated in short-term pair-bonding strategies (Minkov and Bond, 2015) which are useful for reproduction, but a potential obstacle for relationship maintenance. Dopamine is also involved in pair-bonding in voles (Young et al., 2011) and dopamine-rich brain sites have been shown in association with both early-stage and long-term love (see Acevedo, 2015, review). Thus, we examined DRD4 as an indicator of the dopamine system's involvement in romantic love, which has been inferred in research on romantic love, but only tested in a few studies (i.e., Takahashi et al., 2015).

Another gene that affects dopamine transmission in the brain is *COMT*. *COMT* codes for catechol-*O*-methyltranferase (COMT), an enzyme which degrades catecholamines, including dopamine, as they are released in the synapse (Männistö and Kaakkola, 1999). *COMT* rs4680, one allelic variant of *COMT*, results in increased COMT activity and thus lower dopamine levels. Individuals with the *COMT* rs4680 A- (versus G) allele variant have decreased COMT activity resulting in higher dopamine levels (Chen et al., 2004). Thus, they show greater reward-seeking behavior and reward responsiveness, and higher subjective ratings of pleasure in response to positive events, compared to those with more G-alleles (Wichers et al., 2007; Lancaster et al., 2012). One study with 120 participants found that individuals with more COMT A-alleles scored higher on the "Temporal Experience of Pleasure Scale" (Gard et al., 2006), which measures trait anticipatory and consummatory positive affect (Katz et al., 2015). These effects were mediated by activation of the prefrontal cortex in the post-reward phase, suggesting links between *COMT* A-alleles and self-reported consummatory positive affect. Furthermore, in a meta-analysis of 51 studies, a greater number of *COMT* rs4680 A-alleles were associated with obsessive compulsive disorder in males (Taylor, 2016). Obsessive compulsive disorder is correlated with dopaminergic activation (Goodman et al., 1990; Denys et al., 2004), and obsessive thinking is characteristic of romantic infatuation which includes intrusive, uncontrollable thoughts about the partner (Tennov, 1999). Thus, we examined *COMT* rs4680 as a marker for sensitivity to dopaminergic action and potentially romantic love.

Building on human and animal studies examining the biological underpinnings of pair-bonding, this study investigated the neural and genetic correlates underlying romantic love maintenance over the first year of newlywed marriages. We measured self-report (Eros scale) and neural (functional MRI) correlates of romantic love among first-time newlyweds, observed around the wedding date (T1) and 1-year after (T2), implementing a scanning protocol used in prior studies examining romantic love (Aron et al., 2005; Acevedo et al., 2011). The fMRI task measured participants' neural activity in response to viewing facial images of their partner versus a familiar, neutral acquaintance. We defined romantic love maintenance as stability in Eros scores (i.e., small change) between T1 and T2. Each individuals Eros difference score (T2-T1) was correlated with brain activations at T1 to determine what brain systems might be predictive of romantic love maintenance, and at T2 to determine what brain systems might be involved in the maintenance of romantic love. We focused our results on the brain activations that were shown at both T1 and T2, but also made available T1 and T2 results in Supplementary Tables.

Also, for the first time in human romantic love studies, we analyzed interactions of romantic love maintenance with genetic polymorphisms (*AVPR1a* rs3, *OXTR* rs53576, *DRD4*-7R, and *COMT* rs4680) implicated in monogamous pair-bonding. We predicted that neural, hormonal, and genetic correlates of pair-bonding found in other mammals, and the brainstem reward/drive system identified in human love studies, would be involved in the maintenance of romantic love over first-year marriages. Beyond advancing the science of pair-bonding, such findings might also benefit couples and therapists through a deeper understanding of the processes that sustain romantic love.

MATERIALS AND METHODS

Participants

Participants provided informed consent in accordance with the IRB procedures of the University of California, Santa Barbara (UCSB) and Albert Einstein College of Medicine. Subjects were recruited via advertisements, flyers, listservs, and word of mouth. Before undergoing scanning, all participants were interviewed to assess eligibility criteria such as first-time marriage for both partners, no children for either partner, relatively good health, and fMRI contraindications (right-handedness, good health, no metal in or on the body, no claustrophobia, no pregnancy, and no history of head trauma). The eligibility criteria were selected to reduce variability of the sample since this was the first study to examine the physiology underlying changes in romantic love in newlywed marriages. We selected individuals in first-time marriages with no children to mirror animal studies where monogamous mammals solidify pair-bonds prior to producing offspring. All procedures were described at the time of the interview.

The resulting sample was composed of 19 (11 women and 8 men) healthy, right-handed individuals, ages 21 to 32 (27.21 ± 3.29 years), in established relationships (4.11 ± 3.09 years), without children, and living with their partner about 2 years (1.9 ± 1.6 years). At baseline (T1), some participants were recently married (10 married, 1.9 ± 1.5 months), while others were soon to be married (2.6 ± 1.7 months until the wedding). The sample of participants were mostly college-educated: 11 participants had college degrees and 6 had a master's degree or higher, while only 2 had a high-school level education. The mean annual household income of the sample was $62,000 (±$28,000, range $16,000 to $110,000).

Thirteen (seven females and six males) of the 19 participants returned for a second scan (T2), approximately 11.3 months (SD ± 1.3, range 9.0–13.5) after the initial scan (T1). Herein, we report findings that were shown at both measurements (T1 and T2) among the group of 13 participants that were scanned twice.

Procedure

Once eligibility was confirmed, participants provided the experimental stimuli: face images of their partner and a highly familiar neutral acquaintance (HFN). The HFN served as a control for facial familiarity and was matched to the partner by age, sex, and length of time known. The partner-HFN face viewing task has been used in prior fMRI studies of romantic love (e.g., Aron et al., 2005; Xu et al., 2011) and was originally developed in a study showing that images of partner faces, compared to other types of stimuli (i.e., songs and scents), elicited the most intense love feelings among individuals in love (Mashek et al., 2000). All photos were digitized according to standard procedures where only the face was presented, and they were shown with Presentation software (Psychological Software Tools, Inc., Pittsburgh, PA, United States) during the scan.

For the fMRI task, participants viewed alternating face images of the partner and the HFN (shown individually) interspersed with a countback task (displayed individually, for 20 s each). For the countback task (used to reduce carry-over effects of viewing the facial images), subjects were asked to mentally count backwards in increments of seven, starting with a random four-digit number displayed on the screen. The entire session lasted for 12 min, and stimuli (images and the countback task) were displayed for 20 s each. At the start of the session, participants were instructed to recall non-sexual events with the person whose face image would be displayed on the screen. After the scan, participants provided affective ratings while still in the scanner to verify that the evoked emotion corresponded to the target image (see Acevedo et al., 2014 for results of the affective ratings). Identical procedures, questionnaires, and photos were used at T1 and T2.

Questionnaires

Participants completed a battery of questionnaires, including the Eros measure of romantic love from the Love Attitudes Scale (LAS; Hendrick and Hendrick, 1986), the widely used Relationship Assessment Scale (RAS, Hendrick, 1988) for relationship satisfaction, and two items assessing sexual satisfaction and frequency. All measures used a 1–7 item Likert rating scale. Descriptive statistics and correlations are shown in **Tables 1**, **2**.

TABLE 1 | Relationship self-report mean (*M*) and standard deviations (*SD*).

	T1		T2			
	M	***SD***	***M***	***SD***	***T***	***p***
Romantic love	6.33	0.32	6.17	0.87	0.55	0.59
Relationship satisfaction	6.33	0.59	6.35	0.57	0.13	0.90
Sexual satisfaction	5.85	0.90	5.23	1.54	1.28	0.19
Sexual frequency/week	2.95	1.87	1.83	1.25	4.39	<0.01

The LAS measures six different types of love attitudes toward one's romantic partner: romantic love (Eros), obsessive love (Mania), game-playing love (Ludus), friendship-love (Storge), practical love (Pragma), and altruistic love (Agape). The LAS has been shown to reliably measure these six different love factors (Cronbach's α = 0.39 to 0.87; Shahrazad et al., 2012). Here, we report results for the Eros scale since our focus was on romantic love without infatuation/obsession (see Acevedo and Aron, 2009). Sample Eros scale items include, "My partner and I have the right physical chemistry between us," "My partner and I really understand each other," and "I feel that my partner and I were meant for each other" (Cronbach's α = 0.40, 0.72 at T1 and T2, respectively).

The RAS is a seven-item unifactorial measure of relationship satisfaction with items such as, "How well does your partner meet your needs?" and "To what extent has your relationship met your original expectations?" (Cronbach's α = 0.68, 0.89 at T1 and T2, respectively).

Sexual satisfaction was assessed with one item: "How happy are you with your sex life with your partner?" Sexual frequency used one item: "How frequently do you and your partner engage in sexual activity?"

Gene Sampling and Analysis

Subjects provided saliva samples for DNA extraction via Oragene test tubes. Detection of the number of repeats for *AVPR1a* rs3 and the *DRD4*-7R 48 base-pair repeat sequence was performed using fragment analysis, in which repeat sequences are specified using sequence-specific primers and amplified for detection using polymerase chain reaction (PCR). For the present study, PCR was performed on 50 ng of DNA in buffer [100 mM Tris-HCl (pH 8.0), 500 mM KCl, 1.5 mM MgCl2, 0.2 mM dNTP, 0.2 μM of each primer, and 1 unit of TaqPolymerase (Applied Biosystems)]. Cycling conditions were the following: initial denaturation at 95°C for 2 min followed by 30 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 30 s, and extension at 72°C for 45 s, with a 15 min final extension at 72°C. Microsatellite fragment analyses of RS3 and the *DRD4*-7R polymorphism (i.e., identifying the number of repeats for each sequence) were performed using the ABI 3730 DNA analyzer and Genemapper 3.5 software (Applied Biosystems). For *AVPR1a* rs3, the number of repeat sequences was split at the median (M = 335.86 ± 2.87, range = 330.93 – 341.30) to designate each allele as "long" versus "short." The number

TABLE 2 | Correlations among self-report relationship measures and gene polymorphisms in newlyweds.

Variables	1	2	3	4	5	6	7	8	9	10	11	12
(1) Romantic love T1	–											
(2) Relationship satisfaction T1	0.38	–										
(3) Sexual satisfaction T1	0.19	−0.27	–									
(4) Sexual frequency T1	0.55*	0.30	0.24	–								
(5) Romantic love T2	0.21	0.65*	0.09	0.16	–							
(6) Relationship satisfaction T2	0.05	0.83**	−0.27	0.12	0.73**	–						
(7) Sexual satisfaction T2	−0.12	0.30	0.21	0.11	0.74*	0.45	–					
(8) Sexual frequency T2	0.50*	0.33	0.41	0.90**	0.21	0.16	0.28	–				
(9) *AVPR1a* rs3	0.26	0.58*	−0.11	−0.12	0.46*	0.38	0.12	0.04	–			
(10) *OXTR* rs53576	0.29	0.08	0.25	0.12	0.31	0.23	−0.01	0.14	0.07	–		
(11) *DRD4*-7R	−0.81**	−0.37	−0.06	−0.41	−0.27	0.04	0.00	−0.35	−0.33	−0.08	–	
(12) *COMT* rs4680	−0.50†	−0.35	0.33	0.02	0.10	−0.05	0.43	0.14	−0.34	0.38	0.45†	–

*$p < 0.05$, **$p < 0.01$, †marginally significant $p < 0.10$.

of long alleles (0, 1, or 2) was used as a continuous variable in our analyses.

Genotyping of the *OXTR* rs53576 and *COMT* rs4680 SNPs was conducted using the MassARRAY Compact system on a panel of custom SNP assays designed using RealSNP and MassARRAY Assay Designer (Sequenom Inc.). The protocol involved PCR amplification of 10 ng DNA using SNP-specific primers followed by a base extension reaction using iPLEX gold chemistry (Sequenom Inc.). The final base extension products were treated and spotted on a 384-pad SpectroCHIP using a ChipSpotter LT nanodispenser (Samsung). A MassARRAY Analyzer Compact MALDI-TOF-MS was used for the data acquisition process from the SpectroCHIP. The resulting polymorphisms were called using MassARRAY Typer Analyzer v4.0 (Sequenom, Inc.), and the number of G- or A-alleles was used as a continuous variable in our analyses.

Imaging Data Acquisition and Analysis

A 3.0 T Siemens Trio with a 12-channel phased-array head coil was used for the acquisition of blood oxygenation level dependent (BOLD) responses. A single-shot echo planar imaging sequence sensitive to BOLD contrast was used to acquire 37 slices per repetition time (TR = 2000 ms, 3 mm thickness, 0.5 mm gap), with an echo time (TE) of 30 ms, flip angle of 90 degrees, field of view (FOV) of 192 mm, and 64 × 64 acquisition matrix. Prior to the acquisition of BOLD responses, a high-resolution T1-weighted sagittal sequence image of the whole brain was obtained (TR = 15.0 ms; TE = 4.2 ms; flip angle = 9 degrees, 3D acquisition, FOV = 256 mm; slice thickness = 0.89 mm, acquisition matrix = 256 × 256).

Imaging Data Processing

Functional images were subjected to standard preprocessing procedures using SPM5 (Wellcome Department of Cognitive Neurology). First, functional EPI volumes were realigned to the first volume, smoothed with a Gaussian kernel of 6 mm, and then normalized to the T1.nii image template. No participant showed movement greater than 3 mm (whole voxel). After pre-processing, the partner-versus-HFN contrasts were created separately for the T1 and T2 group results.

Multiple Regression Data Analysis

Multiple regression analyses were carried out to estimate group brain activity associated with (a) romantic love difference scores (T2 minus T1) and (b) interactions between romantic love difference scores (T2-T1) with *AVPR1a* rs3, *OXTR* rs53576, *COMT* rs4680 and *DRD4*-7R, examining each gene separately. The effects of *AVPR1a*, *OXTR*, *COMT,* and *DRD4* were tested in separate models. Thus, results are presented for each separate regression. There were no significant differences in sex, age, or relationship length therefore, analyses were conducted without controlling for these variables.

Regions of Interest (ROIs) and Whole-Brain Analyses

Regions of interests for the activations were based on previous studies of romantic love (noted in the table legends). We adopted a false discovery rate (FDR) for multiple comparisons correction (Genovese et al., 2002) at $p < 0.05$. ROIs occupied a 3–10-mm radius with a 3-voxel minimum, depending on the size of the brain area. For exploratory purposes, we conducted whole-brain analyses at $p < 0.001$ (uncorrected for multiple comparisons), minimum spatial extent of $\geq$5 contiguous voxels. All regions were confirmed using the human brain atlas by Mai et al. (2016). **Tables 3–5** report significant effects replicated at T1 and T2 to minimize the risk of false positive findings due to our small sample size. Other results are reported in the Supplementary Tables.

RESULTS

Descriptive Statistics

Descriptive statistics are reported in **Table 1**. The mean change in Eros scores from T1 to T2 ($M = -0.13 \pm 0.89$, range = −3.00 to +0.50) was not statistically significant. Specifically, 75% of the sample showed increases of less than a point, 25% showed no change, and 25% showed decreases of less than a point in Eros scores. Thus, the majority of the sample reported romantic

TABLE 3 | Regional brain activations correlated with romantic love maintenance among newlyweds.

	Left					Right				
Brain Region	***x***	***y***	***z***	***T***	***p***	***x***	***y***	***z***	***T***	***p***
Brain responses replicated at Times 1 and 2										
ROI Activations										
SN, lateral[1]						15	−15	−12	3.97	0.001
Paracentral lobule[2]	−6	−24	57	3.45	0.01					
Whole-brain Deactivations										
Inferior frontal gyrus						54	21	3	4.13	<0.001

All results are for regions showing greater activation in associated with change in Eros scores (T2-T1) over the first year of marriage in newlyweds. Superscripts denote references for ROIs: [1]Acevedo et al. (2011); [2]Wise et al. (2016).

TABLE 4 | Regional brain activations showing interactions with *AVPR1a* rs3 (long alleles) and romantic love maintenance among newlyweds.

	Left					Right				
Brain Region	***x***	***y***	***Z***	***T***	***p***	***x***	***y***	***z***	***T***	***p***
Brain responses replicated at Times 1 and 2										
ROI Activations										
VTA, posterior[1]						6	−21	−21	2.58	0.02
Periaqueductal gray[1]						3	−33	−21	2.87	0.02
Posterior hippocampus[1]						39	−27	−9	3.87	0.01
Occipital cortex, area 17/18[1]						15	−90	3	2.49	0.02
Whole-brain Activations										
Superior temporal gyrus/ Angular gyrus						45	−78	24	4.41	<0.001

All results are for regions showing activation in association with AVPR1a rs3 long versus short alleles and change in Eros scores (T2-T1) over the first year of marriage in newlyweds. Superscripts denote references for ROIs: [1]Acevedo et al. (2011).

TABLE 5 | Regional brain activations showing interactions with *OXTR* rs53576 (G alleles) and romantic love maintenance among newlyweds.

	Left					Right				
Brain Region	***X***	***Y***	***Z***	***T***	***p***	***x***	***y***	***z***	***T***	***p***
Brain responses replicated at Times 1 and 2										
ROI Activations										
VTA/SN[1]	−3	−15	−21	4.43	0.01					
Septum/fornix region[1,2]	0	0	23	3.83	0.01	3	0	24	3.64	0.02

All results are for regions showing activation in association with OXTR rs53576 (G versus A alleles) and change in Eros scores (T2-T1) over the first year of marriage in newlyweds. Superscripts denote references for ROIs: [1]Acevedo et al. (2011); [2]Aron et al. (2005).

love maintenance. Only one participant showed a steep decrease (−3.00 points) in romantic love over the first year of marriage. Thus, we examined the data without the outlier. However, the brain imaging correlations did not change significantly, including the *OXTR, AVPR1a*, *DRD4,* and *COMT* interactions with romantic love maintenance (Eros T2-T1). Additionally, activation of the VTA in response to images of the partner remained positive, but in some cases became non-significant, when the outlier was excluded. Thus, we proceeded with analyses including the outlier because variable values make these results more generalizable to the population. That is, it is expected that some couples will experience steep decreases in romantic love in the early stages of marriage as shown by research reporting "honeymoon effects" (e.g., Huston et al., 2001).

Correlations Among Variables

Correlations among self-report measures are reported in **Table 2**. At each time point, romantic love was significantly correlated with frequency of sexual activity (T1: $r = 0.55$, $p < 0.05$; T2: $r = 0.50$, $p < 0.05$). Romantic love was also strongly correlated with relationship satisfaction: at T1 relationship satisfaction predicted romantic love at T2 ($r = 0.65$, $p < 0.05$), and at T2 relationship satisfaction was correlated with romantic love at T2 ($r = 0.73$, $p < 0.01$). Gene correlations showed that *AVPR* rs3 (long alleles) was significantly correlated with relationship satisfaction at T1 ($r = 0.58$, $p < 0.05$) and with romantic love at T2 ($r = 0.46$, $p < 0.05$). Also, both dopamine polymorphisms, *DRD4*-7R ($r = -0.81$, $p < 0.01$) and *COMT* rs4680 ($r = -0.50$, $p < 0.10$), were negatively correlated with romantic love scores at T1.

Gene Polymorphism Distributions

Gene polymorphism distributions for the sample were as follows: *AVPR1a* rs3 (short = 4, short/long = 6; long = 3), *OXTR* rs53576 (AA = 1, AG = 6, GG = 6), *COMT* rs4680 (AA = 2, AG = 6, GG = 5), and *DRD4*-7R (2 = 2 repeats, 2 = 3 repeats, 7 = 4 repeats, 2 = 7 repeats).

Neuroimaging Results

Neural Correlates of Romantic Love Maintenance

As **Table 3** shows, at both T1 and T2 neural responses to the partner (versus HFN) images showed significant correlations with romantic love maintenance (Eros T2-T1 scores) in the right SN and the left paracentral lobule (PCL) (see **Figure 1A**). Scatterplots show correlations between Eros scores and activity in the right SN and PCL at T2 (**Figures 1B,C**). Significant deactivation at both T1 and T2 was observed in the inferior frontal gyrus (IFG).

Some activations occurred only at T1 or T2, but not both. At T1-only, partner (versus HFN) activations predictive of romantic love maintenance (T2-T1 Eros scores) were observed in the raphe, pons, medial prefrontal cortex, and paracentral lobule (ROIs), as well as the right perirhinal/fusiform, superior frontal gyrus (SFG), superior temporal gyrus (STG) and the left precuneus (whole-brain). At T2-only, partner (versus HFN) activations were significantly correlated with romantic love maintenance (T2-T1 scores) in the right amygdala/globus pallidus (GP) and the left mid-insula (ROIs); and the bilateral occipital cortex, supplementary motor area, precentral gyrus, left and right SFG, and parietal area (whole-brain). At T1-only, a number of deactivations were observed in the right anterior insula (AI), occipital cortex, middle frontal gyrus (MFG), and the left collateral sulcus. At T2-only, deactivations were prominent in the right SFG and the left angular gyrus (AG) (see **Supplementary Table 1**).

Neural Interactions of Romantic Love × *AVPR1a* rs3

As shown in **Table 4**, at both T1 and T2, the interaction of romantic love maintenance with *AVPR1a* rs3 (long versus short alleles) showed significant effects in the right posterior VTA (**Figures 2A–C**), the PAG, posterior hippocampus, occipital cortex (ROIs), and the STG (whole-brain). Scatterplots show the correlations between *AVPR1a* rs*3* and the right VTA response at T1 and T2 (**Figures 2B,C**).

As shown in **Supplementary Table 2**, T1-only partner (versus HFN) activations were predictive of romantic love maintenance as a function of *AVPR1a* rs3 (long versus short alleles) in the right caudate tail, pons, septum fornix, and amygdala/GP (ROIs). At T2-only, interactions with *AVPR1a* rs3 were shown in the left VTA, caudate head, bilateral raphe, hippocampus/caudate tail, posterior hippocampus, left anterior cingulate cortex (ACC), occipital cortex (ROIs), and the right lateral geniculate (whole-brain).

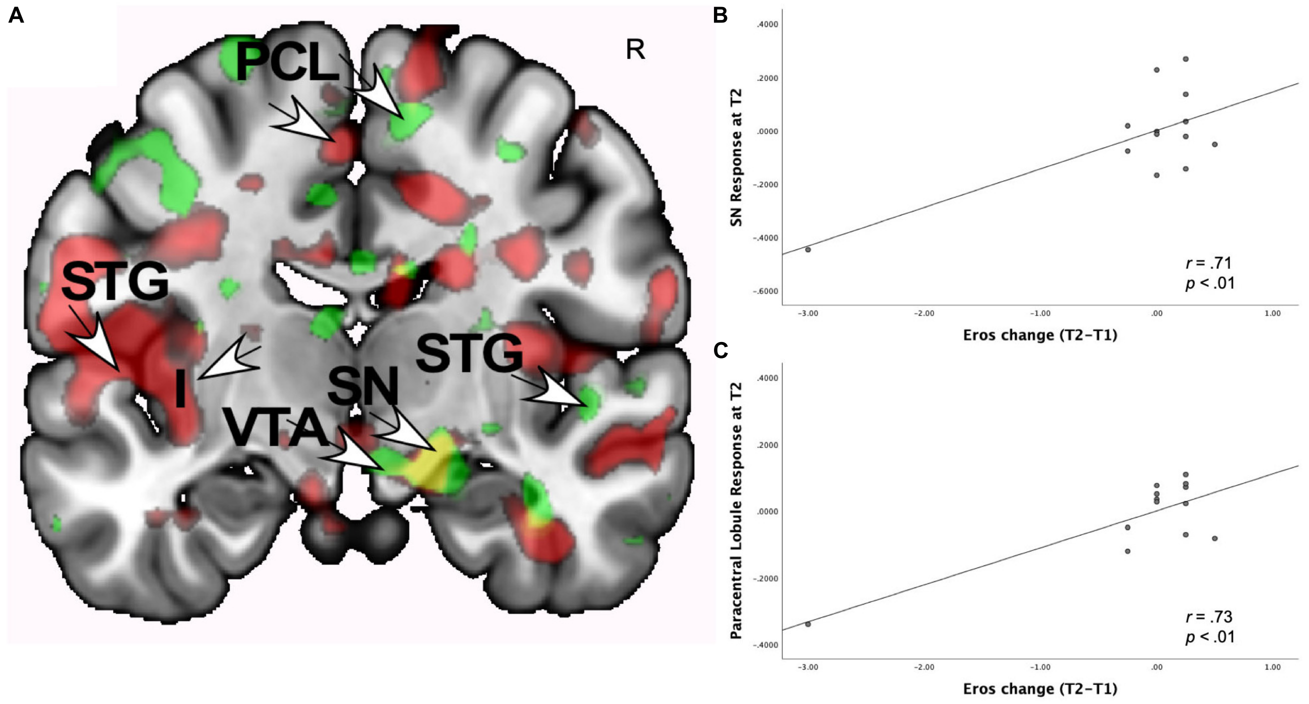

FIGURE 1 | (A) Regional brain activations showing positive correlations with change in romantic love scores (T2-T1: love maintenance) over the first year of marriage among newlyweds in response to viewing face images of the partner versus a highly familiar, neutral acquaintance. Yellow: T1 *and* T2 brain responses in the right SN (arrow). Red: T2 brain responses in the R anterior VTA (arrow) and R STG (arrow). Green: T1 brain responses in the L STG (arrow), and L PCL (arrow). **(B)** Scatterplot shows the correlation between change in romantic love (Eros) scores (T2-T1) and R SN activation at T2. **(C)** Scatterplot shows the correlation between change in romantic love scores (T2-T1) and L PCL activation at T2.

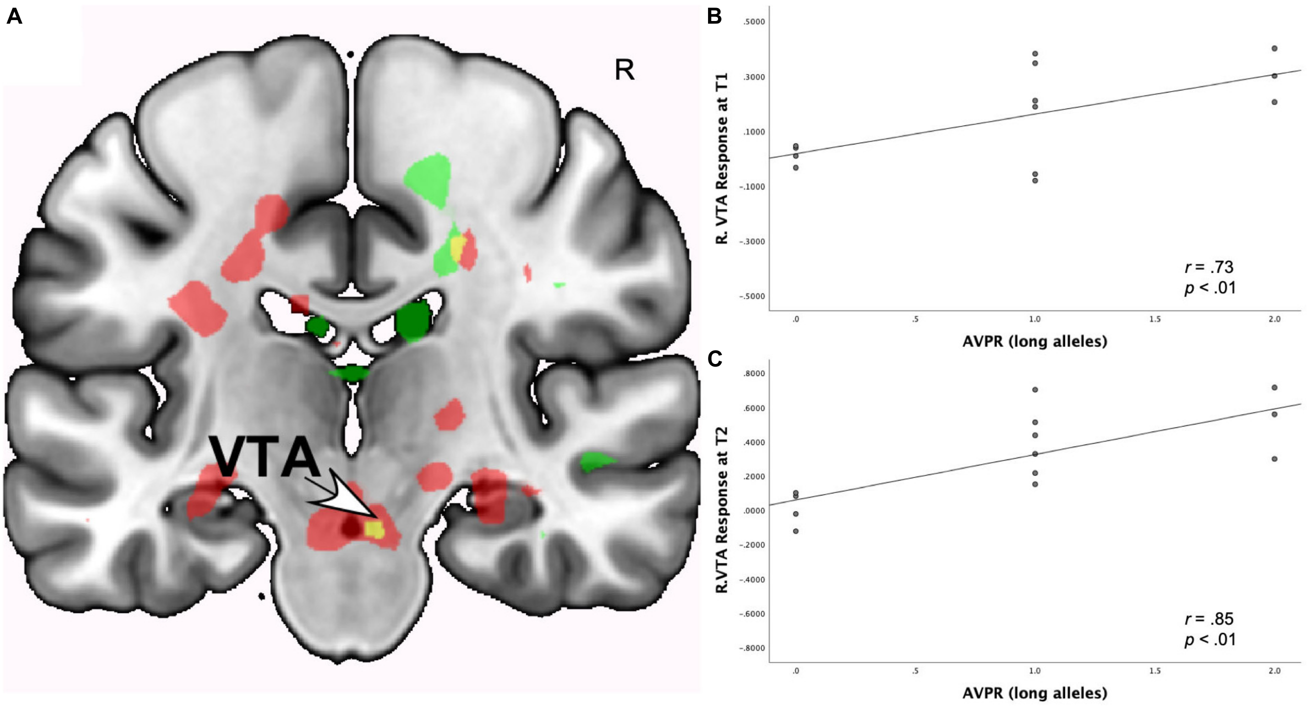

FIGURE 2 | (A) Regional brain response interactions with *AVPR1a* rs3 (long versus short alleles) and change in romantic love scores (T2-T1: love maintenance) among newlyweds in response to viewing facial images of the partner versus a highly familiar, neutral acquaintance. Yellow: T1 *and* T2 brain responses in the R posterior VTA (arrow). Red: T2 brain responses bilaterally in the posterior VTA. **(B)** Scatterplot shows the correlations between *AVPR1a* rs3 (long versus short alleles) and the R VTA response at T1. **(C)** Scatterplot shows the correlations between *AVPR1a* rs3 (long versus short alleles) and the R VTA response at T2.

Neural Interactions of Romantic Love x *OXTR* rs53576

As shown in **Table 5**, at both T1 and T2, the interaction of romantic love maintenance with *OXTR* rs53576 (G versus A-alleles) showed significant effects in the left VTA/SN and bilateral septum/fornix (**Figure 3A**).[1] Scatterplots show the correlations between *OXTR* rs53576 with left VTA responses at T1 and T2 (**Figures 3A–C**).

As shown in **Supplementary Table 3**, T1-only partner (versus HFN) activations predicted romantic love maintenance (T2-T1) as a function of *OXTR* rs53576 (G versus A-alleles) in the right PAG, basolateral amygdala, left central amygdala, hippocampus (ROIs), and the bilateral occipital/lingual gyrus (whole-brain). At T2-only, activations as a function of *OXTR* rs53576 (G versus A-alleles) were observed in the left posterior VP, caudate, right central amygdala (ROIs), and the right intraparietal sulcus, IFG, MFG, STG, and left dorsolateral PFC (whole-brain). Deactivations were evident at T1 in the bilateral SFG and left MFG. At T2-only, deactivations were observed in the left caudate, AG, somatosensory cortex, and bilaterally in the lateral geniculate and premotor cortex.

Neural Interactions of Romantic Love x *DRD4*-7R

As **Table 6** shows, at both T1 and T2, romantic love maintenance was positively correlated with *DRD4* (greater number of 7R alleles) and activity in the left VTA/SN and posterior insular cortex (**Figures 4A–C**). Scatterplots show the correlations between *DRD4*-7R with activation in the left SN/VTA at T1, and the insular cortex at T1 and T2 (**Figures 4A–C**).

At T1-only, partner (versus HFN) activations were predictive of romantic love maintenance as a function of *DRD4*-7R in the bilateral medial PFC, right PCL (ROIs), and the right dorsolateral PFC (DLPFC), entorhinal cortex, left SI, supramarginal gyrus, and lateral PFC (whole-brain). At T2-only, activations as a function of *DRD4*-7R were observed in the left somatosensory cortex and the DLPFC (whole-brain). Deactivation in the left temporal gyrus was evident at both T1 and T2, and at T2 deactivations were observed in the bilateral hippocampus and the right temporal gyrus (see **Supplementary Table 4**).

Neural Interactions of Romantic Love x *COMT* rs4680

As shown in **Table 7**, romantic love maintenance, at both T1 and T2, was positively correlated with *COMT* rs4680 (greater number of A-alleles) and response to partner (versus HFN) images in the left SN/VTA and posterior insular cortex (**Figures 5A–C**). Scatterplots show the correlations between *COMT* rs4680 with the left SN/VTA response at T1, and with insular cortex response at T1 and T2 (**Figures 5A–C**).

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[1] The VTA/SN activation for the *OXTR* rs53576 interaction at T2 was only marginally significant at $p = 0.09$. However, given the strong theoretical and empirical basis for its examination, we noted the VTA replication for Times 1 and 2 in this sample.

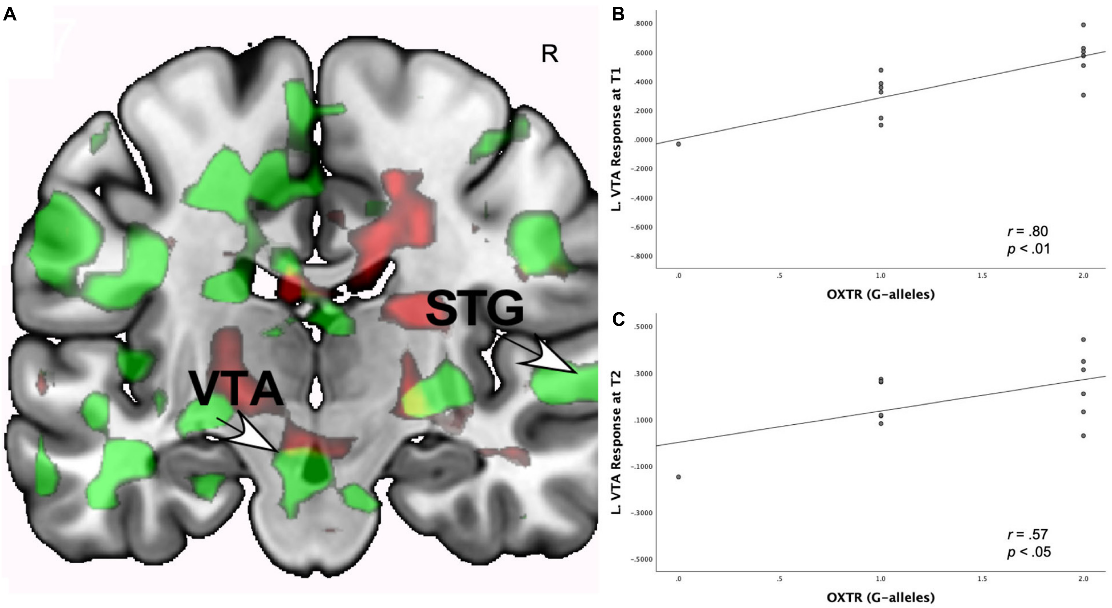

FIGURE 3 | (A) Regional brain response interactions with *OXTR* rs53576 (G versus A-alleles) and change in romantic love scores (T2-T1: love maintenance) among newlyweds in response to viewing facial images of the partner versus a highly familiar, neutral acquaintance. Yellow: T1 *and* T2 responses in a small part of the left VTA (arrow). Green: T1 brain response bilaterally in the posterior VTA/SN. Red: T2 brain response bilaterally in the posterior VTA/SN. **(B)** Scatterplot shows the correlations between *OXTR* rs53576 (G versus A-alleles) and the L VTA response at T1. **(C)** Scatterplot shows the correlations between *OXTR* rs53576 (G versus A-alleles) and the L VTA response at T2.

TABLE 6 | Regional brain activations showing interactions with *DRD4* 7R alleles and romantic love maintenance among newlyweds.

	Left					Right				
Brain Region	**x**	**y**	**Z**	**T**	***p***	**x**	**y**	**z**	**T**	***p***
			Brain responses replicated at Times 1 and 2							
			ROI Activations							
VTA/SN[1]	−9	−12	−9	3.26	0.01					
Insular cortex[2,3]	−45	−12	9	3.85	0.01					
			Whole-brain Deactivations							
Temporal gyrus, anterior	−39	9	−24	6.29	<0.001					

All results are for regions showing activation in association with DRD4 7R alleles and change in Eros scores (T2-T1) over the first year of marriage in newlyweds. Superscripts denote references for ROIs: [1]Acevedo et al. (2011); [2]Aron et al. (2005); [3]Xu et al. (2011).

Supplementary Table 5 shows T1-only partner (versus HFN) activations predictive of romantic love maintenance (T2-T1) as a function of *COMT* rs4680 in the bilateral medial PFC, the right primary sensory cortex, and the left secondary somatosensory cortex (whole-brain). At T2-only, activations as a function of *COMT* rs4680 were shown in the left PCL (ROI); and in the right VLPFC, DLPFC, and posterior cingulate cortex (whole-brain). Additionally, deactivations were observed in the hippocampus at T1, while at T2 deactivations were evident in the SN, caudate tail, and dorsal midbrain.

DISCUSSION

We investigated the neural and genetic (*AVPR1a* rs3, *OXTR* rs53576, *DRD4*-7R and *COMT* rs4680) correlates of romantic love maintenance among first-time newlyweds. Marriage is a pivotal life event that marks the establishment of the family unit, with implications for reproduction, bi-parental care of offspring, long-term companionship, and well-being (Fletcher et al., 2015). Using fMRI, we scanned newlyweds around the time of the wedding (T1), and a subset returned for a second scan about 1 year later (T2). Consistent with research on the neural correlates of long-term romantic love (Acevedo et al., 2011), at both time points, newlyweds showed activation in the dopamine-rich substantia nigra (SN) in association with romantic love maintenance. They also showed dopamine-rich, VTA-related genetic expression in association with *AVPR1a* rs3 (right side), *OXTR* rs53576 (left side), *DRD4*-7R (left side), and *COMT* rs4680 (left side) with romantic love maintenance at both time points. The VTA effects were stronger for *AVPR1a* rs3 long-alleles and *OXTR* rs53576 G-alleles. These genes are associated with complex

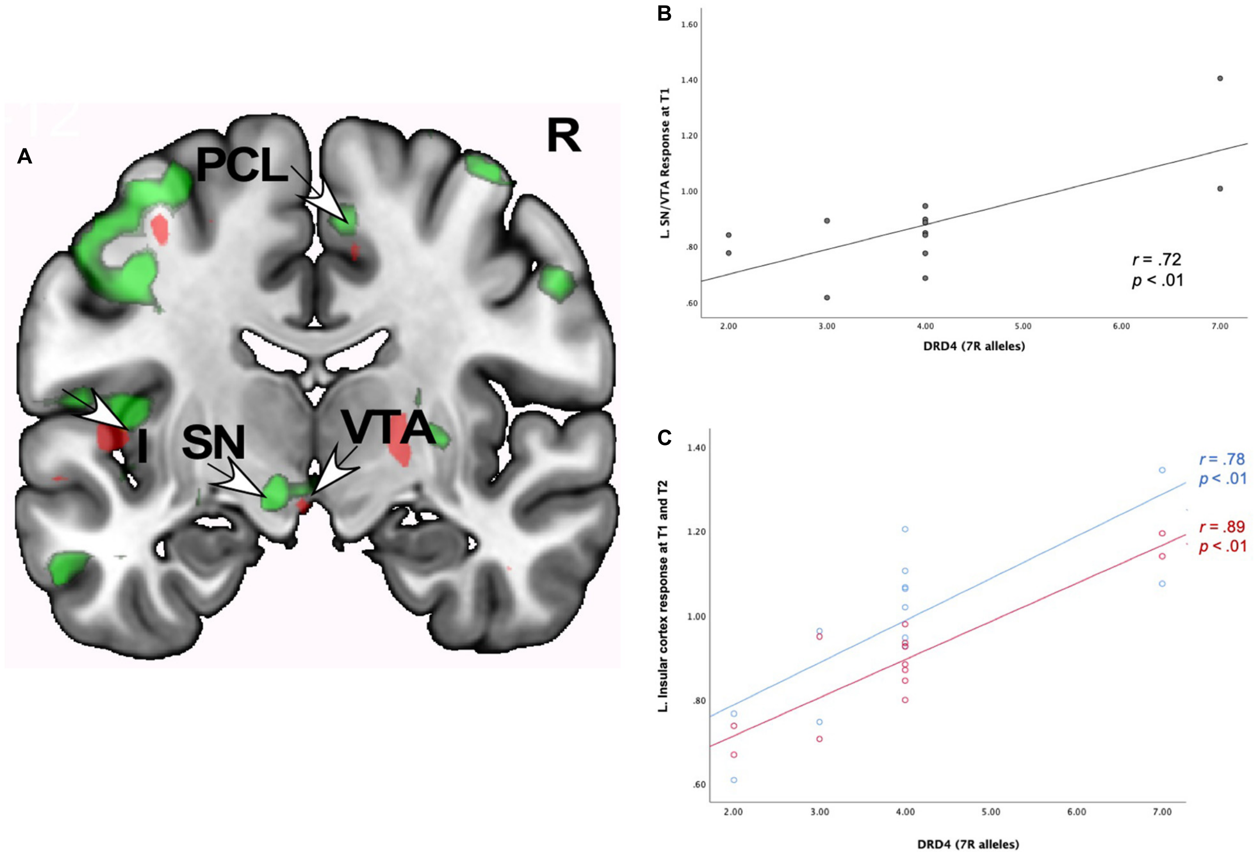

FIGURE 4 | (A) Regional brain response interactions with *DRD4* 7R alleles and change in romantic love scores (T2-T1: love maintenance) among newlyweds in response to viewing facial images of the partner versus a highly familiar, neutral acquaintance. Red: T2 brain responses in the anterior VTA (bottom right arrow) and insular cortex (leftmost arrow). Green: T1 brain response in the anterior VTA/SN (left bottom arrow), insular cortex (leftmost arrow), and R PCL (top arrow). **(B)** Scatterplot shows the correlations between *DRD4* 7R alleles and the L VTA response at T1. **(C)** Scatterplot shows the correlations between *DRD4*-7R alleles and the L insular cortex response at T1 and T2.

social behaviors including pair-bonding (Walum et al., 2008; Li et al., 2015; Gong et al., 2017). Interestingly, the VTA-related *AVPR1a* and *OXTR* effects were observed in a different area, more posterior to those shown for the simple correlation with romantic love maintenance and the dopamine (DRD4 and COMT) genetic interaction effects. This suggests functional segregation of the VTA/SN with different density receptors for OT and AVP compared to dopamine.

The VTA/SN reward regions are involved in coordinating primary behaviors needed for survival and reproduction, such as mating and feeding. They are also involved in secondary reward-processing including responses to monetary gains and addictive substances (Risinger et al., 2005; Fields et al., 2007; D'Ardenne et al., 2008). Largely mediated by dopamine neurons, VTA/SN activity affects reward-seeking, motivation, "wanting," and the drive to "work" for rewards (Berridge and Robinson, 2003). An extensive body of research has shown that dopamine neurons modulate approach-related behaviors, response to novel stimuli, and euphoric experiences (Berridge and Robinson, 2003; Childress et al., 2008; Georgiadis et al., 2010; Schultz, 2010; Krebs et al., 2011; Ikemoto et al., 2015; Noori et al., 2016). Consistent with previous work (for reviews, see Ortigue et al., 2010; Acevedo, 2015), and expanding on it, these findings highlight how the brain's reward system mediates behaviors that are critical for romantic love and its maintenance over time, such as proximity-seeking, positive affect, continued desire, and engaging in relationship-promoting behaviors (such as doing things that make a partner happy).

The present findings also provide the first direct evidence that dopamine-related gene expression in the VTA/SN is involved in the maintenance of romantic love in humans. Previous fMRI studies of romantic love assumed that the VTA response reflected dopamine activation (Aron et al., 2005). Although one study showed dopamine release in the prefrontal cortex while viewing the face of a new romantic partner (Takahashi et al., 2015), here we used genetic markers to confirm direct involvement of dopamine in the midbrain/VTA. Interestingly, our results are consistent with a recent study which showed that dopamine-related gene expression in the VTA of male zebra finches was associated with pair-bonding behaviors (nesting and courtship) of their female pair (Alger et al., 2020). Also, individual differences in social interactions in long-term zebra finch pairs

TABLE 7 | Regional brain activations showing interactions with *COMT* rs4680 (A-alleles) and romantic love maintenance among newlyweds.

	Left					Right				
Brain Region	**x**	**y**	**Z**	**T**	***p***	**x**	**y**	**z**	**T**	***p***
Brain responses replicated at Times 1 and 2										
ROI Activations										
SN/VTA[1]	−6	−12	−12	5.10	0.01					
Insular cortex[2,3]	−42	−18	6	4.56	0.01					

All results are for regions showing activation in associated with COMT rs4680 (A versus G-alleles) and change in Eros scores (T2-T1) over the first year of marriage in newlyweds. Superscripts denote references for ROIs: [1]Acevedo et al. (2011); [2]Aron et al. (2005); [3]Xu et al. (2011).

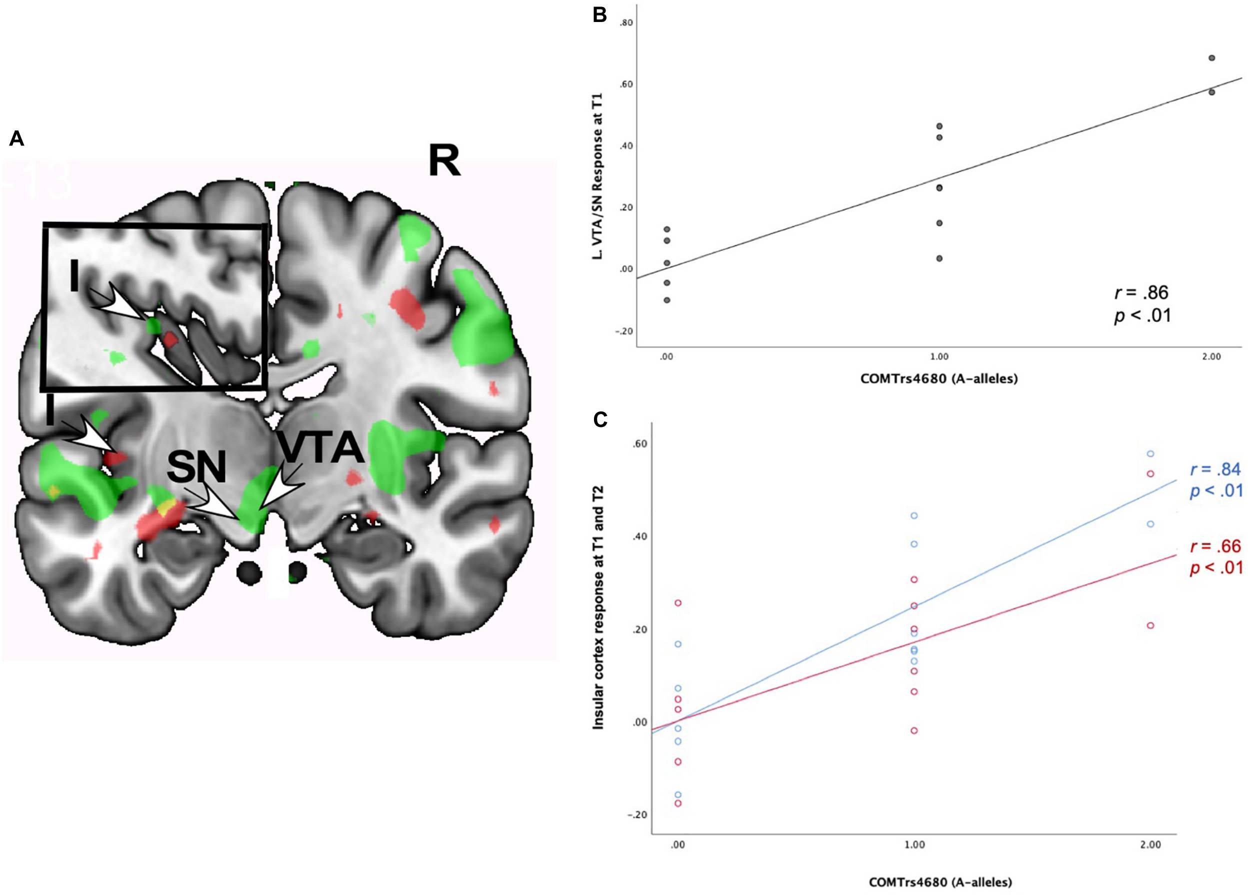

FIGURE 5 | (A) Regional brain response interactions with *COMT* rs4680 (A versus G alleles) and change in romantic love scores (T2-T1: love maintenance) among newlyweds in response to viewing face images of the partner versus a highly familiar, neutral acquaintance. Inset shows a sagittal view of the insular cortex. Green: T1 brain response in the VTA/SN (bottom arrows) and insular cortex (inset). Red: T2 responses in the insular cortex (left arrow and inset). **(B)** Scatterplot shows the correlations between *COMT* rs4680 (A versus G alleles) and L VTA/SN response at T1. **(C)** Scatterplot shows the correlations between *COMT* rs4680 (A versus G alleles) and L insular cortex response at T1 and T2. R, right. L, Left. I, insular cortex; SN, substantia nigra; VTA, ventral tegmental area. Other colored regions did not meet the statistical requirements for whole-brain analysis or were not an ROI. Yellow, significant correlations at T1 and T2. Green, significant correlations at T1. Red, significant correlations at T2.

were associated with the expression of several dopamine-related genes in the VTA. Collectively, these findings highlight the important function of the midbrain VTA region and dopamine for pair-bonding and romantic love.

Additionally, our findings are consistent with the dopamine hypothesis of romantic love (Fisher et al., 2006) and theories suggesting that romantic love is a motivational drive akin to a "natural" addiction (Frascella et al., 2010; Fischer et al., 2016), but also different from drug addiction (Wang et al., 2020). Thus, in addition to advancing knowledge on the biological factors underlying romantic love maintenance, these findings may also be applied to other fields such as the study of the maintenance of "natural" reward/addictions/cravings.

Sex and Romantic Love Maintenance

Other notable findings shown in the present group of newlyweds in association with romantic love maintenance emerged in regions important for sex and sensory processes (the PCL and sensory cortex). Interestingly, the PCL is the genital sensorimotor region activated in women during orgasm and clitoral stimulation (Wise et al., 2016, 2017). Activation of the PCL in the present study is interesting because the primary sensory cortex (SI) usually requires direct tactile stimulation to activate it. There was no stimulation of the genitals in this study, and participants were instructed *not* to think about sexual memories. The traditional textbook understanding of SI function does not include memory, emotion, or person representation, only sensory processing features like pressure. However, studies in recent years suggest that SI may contain memory capacity and a genetically controlled mechanism for cortical memory (Bancroft et al., 2014; Kragel and LaBar, 2016; Muckli and Petro, 2017; Galvez-Pol et al., 2018; Kim et al., 2018). Finally, there is substantial evidence that a memory code for *persons and traits* is active in the ventral medial prefrontal cortex, while other cortical areas are also involved in the mental representation of a person (Heleven and Van Overwalle, 2016; Thornton and Mitchell, 2018). We speculate that looking at the face of the marriage partner and thinking romantic thoughts might activate the mental representation of that person, as faces have in other studies (e.g., Thornton and Mitchell, 2018). Additionally, it's likely that that engaging in sexual acts with the same partner over time would activate genital sensory cortex memory storage mechanisms that importantly become part of the mental representation of the partner.

Although many therapists have suggested an important role for sexual activity in maintaining a marital relationship, this is the first time a cortical brain region associated with direct sexual stimulation has been correlated with self-reports of romantic love in marriages while simply thinking (and viewing face images) of a spouse. Further support for the importance of sex emerged from the robust correlations between romantic love scores and sexual frequency and satisfaction ratings at both time points (see **Table 2**).

AVPR1a and Romantic Love Maintenance

Interestingly, the present sample of newlyweds showed significant interactions with *AVPR1a* rs3 and romantic love maintenance, at both time points, in the right VTA (**Figures 2A–C**), the PAG, posterior hippocampus, occipital cortex and the superior temporal gyrus (STG)— regions important for reward, attachment, memory, and visual and sensory processing (Nagy et al., 2012; for a meta-analysis, see Phan et al., 2002; Schultz et al., 2003; Wager et al., 2003). Most of these regions have appeared in the context of long-term romantic love and maternal love (e.g., Acevedo et al., 2011; for review see Bartels and Zeki, 2004; Acevedo, 2015), highlighting the role of attachment in sustained romantic love among newlywed pair-bonders. They are also consistent with research implicating *AVPR1a* in pair-bonding (Walum et al., 2008) and suggest the diversity of the pair-bonding system through its engagement of reward, memory, sensory, visual, and auditory functions.

OXTR and Romantic Love Maintenance

The pattern of replicated interactions for *OXTR* rs53576 with romantic love maintenance were different from *AVPR1a* effects, appearing in the septum (bilaterally) and the left (L) VTA. Activation of L VTA has mostly appeared in studies of facial attractiveness, specifically showing response to smiling and supportive faces (Vrticka et al., 2008). Also, L VTA activation was shown in a study of males given intranasal OT in response to viewing facial images of their female partner (Scheele et al., 2013). Interestingly, when given OT males rated their partners as more attractive, but OT did *not* affect attractiveness ratings for a familiar matched control. These findings suggest that OT-related effects are partner-specific, thus facilitating attachment and pair-bond solidification. It should be noted that although we did not test for sex differences, sex may influence how OT affects mate choice and pair-bonding (Xu et al., 2020). Also, individual differences, such as personality and attachment style, may influence how OT interacts with pair-bonding choices (Pearce et al., 2019).

Activation of the septum—which is rich in binding sites for OT and, to a lesser extent, AVP—is consistent with animal studies showing that the septum is critical for pair-bond establishment (Liu et al., 2001). In humans, activation of the septum has been implicated in early-stage and long-term romantic love (Aron et al., 2005; Acevedo et al., 2011), and it was specifically associated with obsession-related items of the Passionate Love Scale (Hatfield and Sprecher, 1986) among long-term pair-bonders. We add to this body of work, showing OT's effects in romantic love maintenance.

Dopamine Gene Polymorphisms *(DRD4* and *COMT)* and Romantic Love Maintenance

Robust neural activations were positively correlated with romantic love maintenance and dopamine polymorphisms (*DRD4*-7R and *COMT* rs4680) in the L VTA/SN region and the posterior insular cortex at both time points. As noted above for the *OXTR* findings, the L VTA is specifically activated in response to facial attractiveness (e.g., Aron et al., 2005; Liang et al., 2010). Interestingly, the *DRD4*-7R genetic polymorphism, which is associated with reduced binding for dopamine and greater novelty seeking, was *negatively* correlated with romantic love scores at T1. Individuals with the 7R allele show higher rates of promiscuity and novelty seeking (He et al., 2018, meta-analysis; Munafo et al., 2008, meta-analysis; Garcia et al., 2010). Thus, it is not surprising that in the present study, individuals with the *DRD4*-7R variant showed lower romantic love scores but higher activation in the L VTA, where facial attractiveness promotes activation (Aharon et al., 2001; Winston et al., 2007). Dopamine-related gene expression (*COMT* and *DRD4*) in the L VTA suggests that facial attractiveness, reward, and more generally attraction mechanisms may be fruitful areas of examination for future research on sustaining romantic love in marriages.

COMT and *DRD4* also showed significant interactions in the insular cortex which is involved in a variety of functions including reward, emotion, social bonding, sensory processing, and self-awareness (for review see Gogolla, 2017). Specifically, the posterior insular cortex area where *DRD4*-effects were shown, is implicated in social support networks in elderly individuals (Cotton et al., 2019), making this an interesting region for future investigations of relationships. The human insula has also become a target for treatment in a variety of disorders such as substance abuse, depression, anxiety disorders, schizophrenia, and autism. Specifically, dopamine and opioid receptors in the insular cortex are thought to influence addiction (Ibrahim et al., 2019). Our findings highlight the role of attachment in sustained romantic love and are consistent with theories suggesting that romantic love is a "natural addiction" (Fischer et al., 2016).

Collectively, activation of the insula and other regions identified here (e.g., the STG, occipital area, hippocampus, PCL involved in sensory processing) are consistent with the idea that romantic love is an emergent property of pair-bonding whereby multi-sensory information is translated into processes such as communication, empathy, and decision-making as well as complex cognitive processes such as imagining a future together (Walum and Young, 2018). Thus, basic reward, sensory and higher-order cortical processes and their intersections, as exemplified herein, are critical for the maintenance of romantic love in established pair-bonds.

Deactivations Associated With Romantic Love Maintenance

Deactivations emerged in association with romantic love maintenance, at both time points, in the inferior frontal gyrus (IFG) and the temporal gyrus. The IFG plays an evaluative role in multisensory stimuli and may be deactivated when evaluative processes are not engaged (Ethofer et al., 2006; Schirmer and Kotz, 2006). These results are consistent with previous brain imaging studies suggesting that in romantic love, suspension of negative judgment occurs, coinciding with deactivation in the temporal lobe (Zeki, 2007; Xu et al., 2011; Wang et al., 2020). IFG deactivation has also been associated with impairment in stopping a task once initiated (Chambers et al., 2006), consistent with the persistence of romantic love in the present sample.

Future Directions and Limitations

Although this is the first study to provide evidence of the neural and genetic correlates of romantic love maintenance in a sample of newlyweds, it is important to recognize some limitations. The major limitation of this study is the small sample size. Although Friston et al. (2013) argued that small samples have advantages, small sample sizes and low statistical power may contribute to inflated effect sizes. Many of the effect sizes reported here were moderate to large, but with a larger sample in future studies effect sizes may be smaller. However, we relied on region-of-interest analyses and predicted/planned comparisons, which reduces possible statistical errors. Most importantly, many of our key findings were replicated. Replication is the most important statistical procedure for reliability of a result, and many of our key findings were shown at both time points. Also, a strength and a limitation of the study is the homogeneity of the sample.

Constraining the variables in the sample is important for the reproducibility of the results, but renders the results applicable to a limited population. Thus, generalizability of results is another limitation, as the participants in the present study were mostly well-adjusted, in-love, and highly satisfied with their relationship partner at T1. Nevertheless, this group of newlyweds experienced common marital concerns including the balancing of dual careers, managing domestic chores, and financial issues (Lavner and Bradbury, 2010). Also, in line with theories of "honeymoon effects," one participant showed a steep decline in marital satisfaction and romantic love over the first year of marriage. Thus, it will be critical for future research to recruit larger and more diverse samples to capture the full range of relationship trajectories and pair-bonding strategies.

Another issue was that although we replicated many key findings at T1 and T2, other effects emerged separately for T1 and T2. For example, romantic love at T1 showed significant correlations in regions that are rich in serotonin (raphe and pons), while at T2 the patterns of neural activation were more robust in regions associated with emotion processing and rich in opioid receptors (amygdala and GP). Indeed, there were differences after 1 year of marriage that might indicate changes in attitude toward the partner, additional experiences with partner, envisioning a future together with children, conflict, and general life experiences. However, we refrained from speculating on what these differences in activation (and deactivation) might represent, but we did include the results so that future studies with larger samples (that may use different statistical approaches) may form hypotheses and determine if the neural mechanisms underlying romantic love, and its maintenance, change in consistent ways as a function of time.

To this point, it will be important for future studies on the biological basis of pair-bonding and romantic love to recruit couples with diverse levels of relationship quality. Relationship studies are often biased with positive couples because distressed/conflicted couples are more difficult to recruit as romantic partners often feel uncomfortable disclosing negative thoughts, sentiments, and doubts about their relationship. Additionally, social desirability effects may be especially strong around the time of the wedding; thus, appropriate measurement and objective markers are important for capturing couples that may be particularly vulnerable to conflict and sharp decreases in relationship quality.

In the current study we focused on four genes that have been implicated in social behaviors, including pair-bonding. There is a strong empirical basis for examining the particular genetic polymorphisms. For example, the dopamine receptor variant *DRD4*-7R, which we assessed in the present study, is associated with reproductive sexual behaviors (Eisenberg et al., 2007), desire for a wider variety of sexual behaviors (Halley et al., 2016), and higher rates of promiscuous behavior and infidelity (Garcia et al., 2010). However, there are other possibilities to explore. It will be critical for future research to examine a wider array of genetic polymorphisms underlying pair-bonding with larger samples, both with genome-wide association studies (GWAS) and more directed approaches with predicted polymorphisms. It has been shown that in many cases single genes have very small effect sizes (for review, see Fox and Beevers, 2016). However, GWAS studies are limited in that they require very large sample sizes (Landefeld et al., 2018). Other important genetic variants may also be examined in future studies, for example, the 5-HTTLPR VNTR of the serotonin transporter gene that has been associated with differences in life history strategy and risk-acceptance in mating competition (Minkov and Bond, 2015). Such findings are linked to a broader framework of life history theory than we investigated here, but they are relevant to variation in human mating and pair-bonding strategies (Minkov and Bond, 2015; Pearce et al., 2019).

Also, it is important to note that although identifying biological markers for pair-bonding in group studies is helpful, individual differences must be accounted for. For example, in recent years OT has received significant attention for strengthening pair-bonds (e.g., Quintana et al., 2019). However, responses to OT may vary according to some oxytocin genetic polymorphisms and gender (e.g., Pearce et al., 2019; Xu et al., 2020). Also, results from brain imaging studies indicate that oxytocin genetic variants may influence couples' sociosexual feelings, sexual behaviors, and intimacy (e.g., Acevedo et al., 2019a,b; Pearce et al., 2019).

Finally, although this study is the first to report neural and genetic mechanisms underlying changes in romantic love in first-time newlyweds, it would be beneficial for future neurobiological studies to expand measurements beyond the first year of marriage. This might capture important changes that occur over marital development such as the addition of offspring, career transitions, and increased interdependence that is an inevitable aspect of marriage.

CONCLUSION

Romantic love plays a critical role in relationship initiation, longevity, and individual well-being. However, the biological mechanisms underlying romantic love maintenance in marriages have gone largely unexplored. For the first time, we investigated anatomically specific neural activations together with targeted genetic variants (*AVPR1a* rs3, *OXTR* rs53576, *DRD4*-7R, and *COMT* rs4680) to determine if these polymorphisms are associated with romantic love maintenance among newlyweds. Our results show that romantic love may be sustained via genetically influenced processes in widespread reward, emotion, and primary sensory regions of the human brain. Taken together, these findings suggest an important role for mammalian attachment and reward mechanisms in generating high-quality pair-bonds resilient to declines in romantic love over time. In addition, the current study provides initial evidence of how genetic polymorphisms mediate variability in behaviors related to romantic love maintenance and pair-bonding during the first year of marriage. Finally, the results are consistent with the overall hypothesis that romantic love is part of a suite of human reproductive strategies, particularly long-term ones, and a developed form of a mammalian drive to pursue and keep preferred mates. This view, along with these findings about genetic variability, can be therapeutically useful by placing romantic love and its maintenance in a larger context than the individual couple seeking help.

AUTHOR'S NOTE

The data utilized for the current study were part of a broader project (see Acevedo et al., 2014, 2019a,b for other papers), and these results have been published elsewhere (Acevedo et al., 2014, 2019a,b). No analyses in the present research are redundant with any published findings.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation, to any qualified researcher.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by IRBs of the University of California, Santa Barbara and Einstein College of Medicine. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2020.00634/full#supplementary-material

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Manipulation of Self-Expansion Alters Responses to Attractive Alternative Partners

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Past behavioral research has examined relationship infidelity as a potential outcome of focusing on attractive alternative partners when already in a relationship. The extent to which individuals find such alternatives attractive has been shown to be associated with various factors in the relationship, including self-expansion. However, no previous research has tested the role of self-expansion experimentally. This paper presents two experiments that directly manipulate self-expansion to determine the effect of self-expansion on responses to attractive alternative partners. Participants primed to experience a higher need for self-expansion had better memory for attractive alternatives with self-expanding traits dissimilar to their partner's versus attractive alternatives with self-expanding traits similar to their partner's. Additionally, participants primed with self-expansion (via a video of their partner discussing ways in which life with one another is exciting, novel, and challenging), had less fMRI BOLD response to attractive alternatives of the opposite sex in regions associated with perception of attractive faces (anterior cingulate and medial prefrontal cortex) relative to when they were primed with love (via a video of their partner discussing times they felt strong feelings of love for one another), or neutral content (via a video of their partner discussing some times in which they engage in mundane, routine activities together). The magnitude of this effect in the ACC correlated with relationship closeness as measured by the inclusion of the other in the self scale.

Keywords: close relationship, attention to alternatives, self-expansion, romantic love, social neuroscience

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MANIPULATION OF SELF-EXPANSION ALTERS RESPONSES TO ATTRACTIVE ALTERNATIVE PARTNERS

Focusing on attractive alternative partners when one is already in an established pair bond can lead to several negative outcomes, including infidelity and relationship dissolution (for a review of the infidelity literature, see Tsapelas et al., 2011). The extent to which individuals attend to and remember such alternatives, however, may be affected by various factors within the relationship, including love for the partner and self-expansion in the relationship. In the last 30 years, researchers from a wide array of disciplines have studied various correlates and predictors of infidelity, including individual difference and demographic variables (e.g., attachment style, gender), and characteristics involving the primary relationship (e.g., love, satisfaction, commitment). Further, the underlying processes involved in infidelity have been approached from a variety of theoretical perspectives, including evolutionary, attachment, and investment theories, and, most recently, self-expansion model.

INTRODUCTION

Self-Expansion Model

Aron and Aron's (1986) self-expansion model of close relationships posits that people are motivated to enter relationships in order to enhance the self and increase self-efficacy. The main way that people seek to expand the self in the context of relationships is by "including others in the self" (IOS). Over time, the other's resources, perspectives, and identities are integrated into one's own self-concept. These principles have received considerable research support and have been applied to the study of various relationship issues, including romantic love, intergroup relations, breaking up, and relationship boredom (for a review, see Aron et al., 2013).

The self-expansion model suggests that in the beginning phase of a relationship when forming a pair bond (especially rapidly coming to include the partner in the self) is highly self-expanding. This rapid self-expansion is associated with feelings of great pleasure, arousal, and excitement. As time passes, the relationship becomes more predictable and there can be a decline of self-expansion. This decline in self-expansion may be a key factor in the typical decline in relationship satisfaction over time (e.g., Bradbury et al., 2000). Empirical work indicates that a loss of excitement may be a major driving force behind declining relationship quality (e.g., Tsapelas et al., 2009). Because alternative partners' offer novelty, new opportunities for self-expansion, and excitement, declines in self-expansion may be an important contributor to relationship infidelity.

In a sample of dating college students Lewandowski and Ackerman (2006) found that self-reported self-expansion variables (current and potential self-expansion from the relationship and inclusion of the partner in the self) accounted for a large portion of the variance in self-reported susceptibility to infidelity (i.e. likelihood that participants would engage in various infidelity behaviors). Further, VanderDrift et al. (2007) found that reported lack of relationship-derived self-expansion increases attention to alternatives, and decreases devaluation of alternatives. A combination that is likely to promote infidelity.

Other work (Le et al., 2009) examined the relative strength of relationship closeness (IOS) and self-expansion opportunities in predicting sexual infidelity. In a sample of college student participants, self-expansion but not closeness, significantly predicted less sexual infidelity. The same results were found in a second study of college students over a 4-week winter break. This work highlights a distinction between the process of self-expansion and the state of self-other inclusion.

The distinction between self-expansion and inclusion of the other in the self is most clear as a distinction between process, outcome, and the emotional content of each. Self-expansion refers to the process by which one develops new aspects of the self through the relationship. Critically, learning of this type will be dependent on the mesocorticolimbic dopamine system (see Adcock et al., 2006), which is central to predictive reward and motivation (Berridge, 2012). Moreover, greater activity in this dopamine system is associated with romantic love (Fisher and Brown, 2002) and feelings of excitement and desire. Because self-expansion theoretically involves learning, motivation, and reward, self-expansion is a hot process that contributes to intense emotion and promotes attraction to and desire for the partner.

Inclusion of the other in the self, alternatively, is about relationship closeness and is often an outcome of the interpersonal interactions driven by self-expansion. Inclusion of the other in the self is much more strongly related to already formed memories, habits, and patterns of living. A close relationship partner becomes integrated into the way an individual regulates their own need and desires (Saxbe et al., 2019), forming a regulatory system that is dyadic rather than individual in nature. Within this system the individual includes the partner in their planning and resources. Via this cognitive organization, the partner is integrated in person's cognitive systems such that they are included in the person's self-concept. This type of self-other integration is typically cooler once completed and will involve much less emotional content as long as the dyad is relatively predictable and maintains stability. Thus, inclusion of the other in the self is likely a commitment magnifying phenomenon, but relative to self-expansion is a cool psychological process, and therefore not the same as hot processes like self-expansion and romantic love.

Romantic Love and Attention to Alternative Partners

Romantic love also seems to reduce attention to alternatives, and perhaps deters infidelity. Maner et al. (2008) found that priming thoughts and feelings of romantic love for one's current partner reduced attention to photos of physically attractive alternatives in a visual cueing measure. In this study, participants were assigned to either a romantic love condition (in which they wrote a brief essay about a time they experienced strong feelings of love for their current partner) or a control condition (in which they wrote about a time they felt extremely happy). After writing the essay, participants completed a version of the visual dot-probe procedure which assessed how efficiently they were able to shift their attention away from one stimulus location to another. Participants primed for romantic love (compared to those in the control condition) demonstrated less visual attention to the photos of attractive alternative partners.

A later study (Maner et al., 2009) used the same visual cueing task with two different implicit manipulations intended to prime mating: In study 1, participants were primed with words highly relevant to mating (e.g., kiss, lust) and in study 2, participants completed a sentence unscrambling task with words highly relevant to mating. Single participants responded to the mating primes by increasing attention to physically attractive alternatives, but participants in a committed romantic relationship were inattentive to those alternatives. Another study (Gonzaga et al., 2008) found that romantic love (but not sexual desire) led participants to display poorer memory for characteristics of an attractive alternative, specifically attractiveness-related details (e.g., fitness and beauty cues) but not attractiveness-irrelevant details of the alternative. Further, romantic love, but not sexual desire, predicted greater commitment to the current partner.

Perceiving and focusing on desirable alternatives weakens relationship satisfaction and stability, so individuals who are motivated to maintain their relationships will either be inattentive toward alternatives and/or perceive alternatives as less desirable. In contrast, partners lower in love may be more likely to attend to and be attracted to alternatives. Theoretically, self-expansion through a relationship partner may be critical to promoting derogation and decreased attention to alternative partners, but to our knowledge no experimental work has demonstrated a causal effect of self-expansion on attention to alternatives.

The Present Research

Recent behavioral research has indicated that self-expansion and IOS (inclusion of other in the self) play an important role in the perception and evaluation of attractive alternatives. However, this work has entirely been correlational. The present research expands this work in several key ways. Most importantly, no previous research has studied the role of self-expansion experimentally. Both of the present studies specifically manipulate self-expansion (and do so, in two different ways). No previous studies have examined the prediction from the self-expansion model that under conditions of general high self-expansion need, potential alternative partners would be especially salient who have desirable characteristics (which could thus be included in the self if one had a relationship) that the current partner does not have. This is the focus of Experiment 1. Finally, no previous research has examined the role of self-expansion on attention or attraction to potential alternatives. Experiment 2 does so via neuroimaging, which can help distinguish whether self-expansion simply decreases attention to alternatives or whether it decreases actual attraction via the activity of dopaminergic systems. This is a key contribution of Experiment 2. Experiment 2 is also pioneering in that (a) it manipulates degree of self-expansion in the relationship and (b) manipulates degree of relationship love as a comparison condition.

EXPERIMENT 1

Research from the self-expansion model indicates that if one's primary relationship is not meeting self-expansion needs, individuals may look outside the relationship to fulfill these needs. Specifically, the model predicts that if one is feeling that one's self-expansion needs are not being met, the most desirable alternatives would be ones who possess traits one's long-term partner does not. In contrast, if one is feeling adequate self-expansion, and circumstances (such as opportunity) led to an interest in alternatives, the most desirable would be ones that are actually possessed by one's current partner. In this case, one will presumably not need additional and varied forms of self-expansion from a potential alternative, and will instead prefer traits representative of his or her partner.

This experiment is the first of which we are aware to directly investigate how general self-expansion needs influence the way people process information about specific types of alternative partners. We hypothesized that a primed need for self-expansion in one's life will predict greater attention to, and memory for, attractive alternatives that possess self-expanding traits the partner does not have (versus attractive alternatives with self-expanding traits the partner does have).

METHOD

As part of an on-line "mass-testing" session, participants in a current relationship rated various traits for the degree they were possessed by their partner and for how desirable those traits are in general in a romantic partner. At a subsequent, supposedly unrelated, laboratory session, participants were primed with either high or low need for self-expansion, then participated in a task designed to assess memory for and attention to several potential attractive relationship alternatives, some of whom had desirable traits possessed by their current partner, and some with desirable traits not possessed by their partner. Thus, the design was a 2 (high vs. low primed self-expansion need) × 2 (partner-similar versus partner-dissimilar traits) between-subjects design.

Participants

149 participants (111 women, 38 men) recruited from the Stony Brook University Psychology Department subject pool received course credit for their participation. All participants were in a committed, exclusive relationship of at least 6 months; mean age, 19.76; mean relationship length, 22.91 months; 87.9% exclusively dating; the remainder were either married or engaged.

Partner Attributes

In the initial online mass-testing session, participants rated 48 desirable and potentially self-expanding traits, first for how representative each was of their current partner, and second for how desirable each trait would be in a potential romantic partner. These measures were separated by a substantial number of other questionnaires, which reduced potential carryover effects. Example traits included "ambitious," "funny," "talented," "sensitive," "creative," "musical," and "intelligent"–traits rated high in general "likeability" in previous research (Anderson, 1968). The questionnaires completed between the two focal ratings included a number of short-form versions of standard relationship measures.

Before the lab session, for each participant, attributes the participant had rated as highly desirable in a general partner (>7 on 1–10 scale) were used to create 10 target pairings, each trait with a photo of an attractive, opposite-sex face. There were 10 photos total–5 associated with traits the participant had rated characteristic of the partner; 5 with traits the participant had rated as not characteristic of the partner. The 10 attractive, opposite-sex faces were adapted from past research (e.g., Maner et al., 2008, 2009). Mean attractiveness ratings (1–7 scale) were 4.16 for female photos, and 4.06 for male.

Thus, photos of attractive, opposite-sex faces were each paired with an attribute purportedly describing the alternative, designed by the researchers to reflect either (a) potentially self-expanding attributes rated as highly desirable that the participant's actual partner possesses or (b) potentially self-expanding attributes rated as highly desirable that the participant's actual partner does not possess. Traits of each type were randomly paired with photos, separately for each subject. No differences in mean desirability were found for partner-similar vs. partner-dissimilar traits.

Procedures

In the lab session (approximately 2–3 weeks after mass-testing) participants were randomly assigned to either a high or low self-expansion need condition (i.e. how much self-expansion one feels they are experiencing in life in general) employing a priming manipulation used in prior research (see Wright et al., 2004). First, they completed a short self-description and bogus personality test. In the high self-expansion need condition, participants were told that their responses to the personality test indicated that their life was rather predictable and stagnant – that they were in a bit of a "rut," and they demonstrated concern they were not getting the resources needed to meet potential upcoming challenges. In the low self-expansion need condition, participants were told that the test indicated they had recently experienced considerable psychological change, they were somewhat overwhelmed with the number of new things they were trying to manage in their life, and they probably needed time to sort out these changes.

Next, participants were asked to take part in a memory task, as part of an experiment ostensibly having nothing to do with relationships, alternatives, or their own relationship. They viewed photos of 10 attractive, opposite-sex faces, each paired with a trait. Prior to viewing the trait/photo pairs participants were told that they would take part in a subsequent memory test so they should try to remember as many of the photo-attribute pairings as possible. Participants then completed a dot-probe computer task used to measure visual attention to attractive alternatives (for a complete description, see Maner et al., 2008 or Maner et al., 2009). Finally, following the attention task, approximately 12 min after initially encoding the photo/trait pairs, participants were tested on their recall for the attribute-photo pairings by viewing each of the 10 photos (10 s each) on a computer screen and listing (on paper) the associated trait for each photo. The dependent variable was the number of correctly recalled traits (out of a possible 5) for each target type (partner-similar, partner-dissimilar). (At debriefing, no participant identified the experiment's true purpose or its relation to earlier ratings).

RESULTS

To test the key research questions, we employed a 2 × 2 × 2 mixed-design ANOVA with self-expansion need (high vs. low; between subjects), gender, and partner-similar versus partner-dissimilar traits (within-subjects variable) as factors. The condition × partner trait interaction was significant, $F(1, 145) = 12.04$, $p = 0.001$, $\eta^2_p = 0.08$. As shown in **Figure 1**, participants primed for high self-expansion need, $t(73) = 2.05$, $p = 0.04$, correctly recalled more partner dissimilar ($M = 3.22$, SE = 0.21) than partner similar traits ($M = 2.77$, SE = 0.20); those primed with low need, $t(75) = -3.02$, $p = 0.004$, recalled more partner similar ($M = 3.54$, SE = 0.19) than dissimilar traits ($M = 3.11$, SE = 0.21). No other main or interaction effects (including those for gender) were significant.

We also conducted a similar analysis with dot-probe response-time as the focal DV. No main or interaction effects approached significance.

EXPERIMENT 1 DISCUSSION

This was the first study of which we are aware to examine self-expansion needs on the way people process information about alternative relationship partners. When experiencing high need for self-expansion, people displayed better memory for potential alternatives that have desirable traits their partner does not possess. In contrast, those experiencing sufficient self-expansion in life, have better memory for potential alternatives that have desirable traits their partner does possess.

This work suggests a central role for an individuals' state degree of self-expansion motivation in relationship cognition, particularly cognitive processes involving the perception of alternative partners, and perhaps even infidelity. If self-expansion needs are not being met, an alternative's potentially self-expanding traits may be more appealing than such traits of the partner (which are presumably already contributing to the individual's self-expansion); the alternative may be attractive due to the new and varied forms of self-expansion (and new traits to include in the self) that he or she can offer. However, when self-expansion needs are already being met, individuals may not feel it necessary to look outside the relationship for additional self-expansion opportunities, and may focus more on the self-expanding attributes of the partner. Or if situations promote an interest in alternatives, they are likely to be alternatives like the partner one already has.

Another way to interpret these results is that partner's traits matter most: If one needs more self-expansion, it may seem that the traits one's partner has do not add much to life; but if one's life is highly self-expanding, if the possibility of alternatives arises, one may want more of what is already working.

At the same time, a limitation of the present findings, is that we did not find parallel results using a standard attentional

FIGURE 1 | Depicts the mean recall for partner-similar and partner-dissimilar traits in the high and low self-expansion need conditions with 95% confidence intervals.

task that has proven successful in several previous studies of interest in potential alternatives (e.g., Maner et al., 2008). That is, although the predicted pattern was found for memory, it was not significant for attention. This may indicate that attractive alternatives do capture earlier attention, but later processes involved in sustained attention, encoding, and evaluation are modified by self-expansion in the current relationship. If self-expansion is high, individuals may avoid encoding information regarding alternatives as less important because their needs are well served in their current relationship. Such a pattern makes sense if desire for the current partner suppresses desire for alternatives. In animal models there is evidence that increasing the incentive salience of one target can diminish the incentive salience of other targets (DiFeliceantonio and Berridge, 2016) as measured through behavior and the activity of dopaminergic systems in the brain. Increased incentive salience should improve memory encoding and attraction. Fortunately, there are well known neural systems involved in incentive processes, making exploring this question possible using function magnetic resonance imaging (fMRI).

EXPERIMENT 2

Experiment 2, sought to investigate the role of self-expansion (and love) in limiting attraction to alternatives at the neural level by investigating incentive responses to attractive alternatives in dopaminergic systems after self-expansion, romantic love, and neutral primes. Given that self-expansion and romantic love are theoretically linked to processes mediated by the mesocorticolimbic system we should see changes in blood oxygenation level dependent (BOLD) response to attractive alternatives in this system when self-expansion and romantic love with the partner are manipulated, Thus, the goal of this study is to determine whether self-expansion and romantic love manipulations modify reward related responses in the mesocorticolimbic system to attractive alternatives. Having a partner who promotes self-expansion and elicits strong feelings of romantic love should be associated with higher incentive salience for the partner (i.e. predictive reward; see Berridge, 2012 for a discussion of incentive salience and the mesocorticolimbic system). Moreover, increasing the incentive salience of a partner should reduce the relative incentive salience of alternative partners through cortical dopaminergic systems (DiFeliceantonio and Berridge, 2016). If self-expansion reduces attention to attractive alternatives, we should see evidence of reduced activity in mesocorticolimbic activation when self-expansion with one's partner is increased.

Interpersonal attraction and romantic love are strongly related to activity in the mesocorticolimbic dopamine system (Fisher and Brown, 2002) which is crtical for learning, motivation, and incentive salience. Much of the neuroimaging work on interpersonal attraction has focused on facial attractiveness. Perceiving a highly attractive face is associated with increased BOLD response in various subcortical and medial prefrontal regions known to be innervated by ventral dopamine pathway (O'Doherty et al., 2003; Winston et al., 2007). A recent meta-analysis (Mende-Siedlecki et al., 2013), indicates that a portion of this pathway including the medial prefrontal cortex and anterior cingulate cortex (ACC), along with the left nucleus accumbens and surrounding caudate reliably discriminate trust responses from attraction responses by activating more strongly to attractive face stimuli. If self-expansion or romantic love diminish attraction or attention to alternative partners, then neural activity in this system should be lower to faces images of alternative partners after primes of self-expansion or romantic love.

METHOD

Participants

Couples were recruited via flyers posted on and off Stony Brook University's campus, emails to listservs and online advertisements on Craigslist and other website advertising the study. Scanned participants were 18 individuals (12 males and 6 females) in heterosexual long-term relationships (at least 2 years). Partners of each of these 18 also participated in the development of the stimuli. Participants ranged in age from 19 to 42 years (M = 24.10, SD = 6.17). Overall, couples' relationship length ranged from 2 to 24 years (M = 3.89, SD = 4.84), and 3 of the 18 couples were either engaged or married, 3 were dating and living together, and 12 were dating and living separately. Three of the 18 participants who were scanned preferred their left hand.

When participants contacted us expressing interest in the study, we scheduled a phone screening session. During screening, we verified that couples met all inclusion criteria and made sure that one partner was willing and able to enter the scanner safely (no history of claustrophobia, head trauma, drug use, embedded metals, etc.). If both members of the couple were safe to enter the scanner, we allowed the couple to decide who would be in the scanner and who would be outside. Participants were made aware that the study consisted of two in-person sessions (where they would both have to come in to Stony Brook University), with the scan taking place during the second session. Participants were initially told that the study focused on general processes in romantic relationships and at the conclusion of the study, were fully debriefed on the specific hypotheses under investigation.

Session I (Pre-scanning)

The fMRI participant (who later was scanned) and his or her partner (who was not scanned) were asked to identify together some ways in which life with one another is exciting, novel, and challenging, and to give specific examples of such experiences (e.g., things they've done together, joint projects). They were then asked the same thing for times in which they felt strong feelings of love for one another (e.g., the day they got engaged or married). They were also asked to describe some times in which they engage in mundane, routine activities together (e.g., grocery shopping, doing laundry). The experimenter then identified specific instances and experiences related to each of the three categories (i.e. self-expansion, love, and neutral/control).

The fMRI participant and the partner were then separated. The partner was then taken into a separate room where he or she was asked to describe the experiences mentioned above in detail as if they were speaking to their partner (the fMRI participant) and recounting the experiences, and specifically to describe how they felt (and how their partner, the fMRI participant, said they felt) during each of the experiences. While they were describing these experiences, they were videotaped and they were aware of the recording. These video clips were then used (in the scanner in session 2) to prime self-expansion, love, and a neutral/control condition. After editing, a total of two video clips (38 s each) were generated for each of the three conditions. Both partners were unaware as to the exact purpose of the video clips in the study and how they would be used.

While the partner was being interviewed, the fMRI participant completed the following questionnaires in a separate room: Experiences in Close Relationships Scale (Brennan et al., 1998), the Relationship Assessment Scale, a short version of the Passionate Love Scale (Hatfield and Rapson, 1987), a short version of the Self-Expansion Questionnaire (Lewandowski and Aron, 2002), a short version of the Investment Model Commitment Scale (Rusbult, 1983), and the Inclusion of Other in the Self Scale (Aron et al., 1992). When the interview was complete, the fMRI participant (who was later scanned) also completed these questionnaires in a separate room.

Session II (Scanning)

Approximately 2 weeks later, the fMRI participants and their partners returned to the lab to complete the second session. The second session was scheduled approximately 2 weeks later to allow time for editing of the video clips and to reduce the likelihood of carryover effects from the first session. The participant had an fMRI (functional magnetic resonance imaging) scan of their brain completed at Stony Brook University's Social, Cognitive, and Affective Neuroscience Center. The partner waited in a separate room within the same building.

During the scan, the participant first viewed 10 s of general instructions, then passively viewed the following stimuli:

a. 12 blocks of videos were followed by 3 photos of faces (sometimes all male, sometimes all female, but never mixed). These photos were successfully used in past studies (e.g., Maner et al., 2008; Maner et al., 2009) to measure visual attention to attractive faces. 4 blocks (38 s videos) per video type (self-expansion, love, neutral), 2 followed by male and 2 followed by female faces (5 s presentations each). Each video type was present in each set of three blocks: first three, second three, third three, and fourth three blocks. There were six blocks prior to a break (60 s), and 10 s countback tasks (counting back from a very large number in increments of 7) after each block. See **Figure 2** for a diagram.

The Attention to Alternatives Scale and a few brief questions on potential infidelity in their relationship (subjective/objective infidelity measure) were also completed by both partners in the second session post-scanning.

Data Acquisition and Analysis

Preprocessing and analysis of fMRI images was conducted via FMRIB's Software Library (FSL) software (Version 5.98[1]; Worsley, 1994). We used FMRIB's Linear Image Registration Tool, an intra-modal correction algorithm tool (MCFLIRTl; Jenkinson et al., 2002), with slice scan time correction and a high-pass filtering cutoff point of 100 s, removing irrelevant signals. BET (Smith, 2002) brain extraction was employed to remove non-brain material, and smoothing involved a 5-mm full

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[1] www.fmrib.ox.ac.uk/fsl

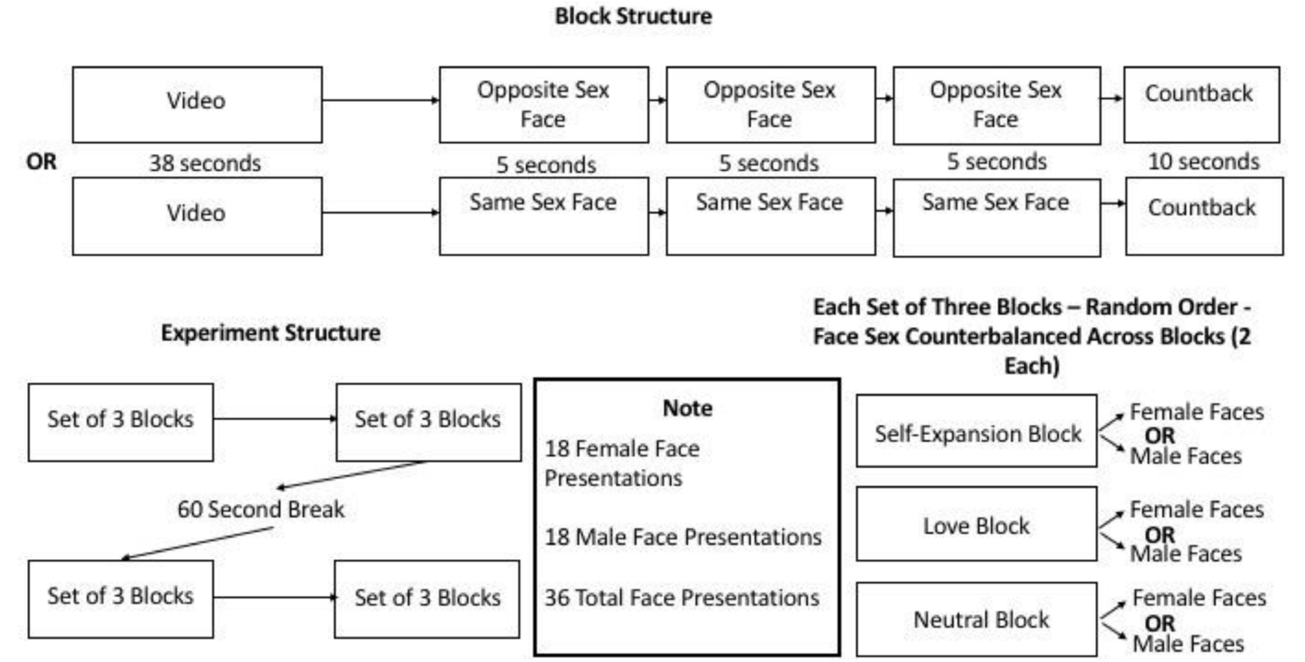

FIGURE 2 | The top of figure 2 diagrams the trial structure of each block. The bottom left of the figure is a diagram of the overall experimental structure broken down by sets of three trials. The bottom right of the figure shows how each set of three blocks includes a block of each video type followed by a set of either female or male faces depending on randomization and counterbalancing. The bottom middle of the figure includes a note on the number of face presentations of each sex.

width at half minimum Gaussian kernel. We registered images to the Montreal Neurological Institute (MNI) space by FLIRT (Jenkinson et al., 2002).

Primary fMRI Data Analysis

Primary analysis was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.98, part of FSL (FMRIB's Software Library see text foot note 1) and time-series analysis by FILM (Worsley, 2001). At the first level of analysis a contrast of opposite-sex image minus same-sex image (OS-SS) was used as the primary contrast. Additional contrasts compared OS-SS between video prime conditions (self-expansion, love, and neutral) contrasting each condition with each other condition. A group level analysis was then employed using FSL Randomize (Winkler et al., 2014), which uses non-parametric methods resulting in better control of type I error rates (Eklund et al., 2016; see also Zhang et al., 2012 for an analysis of the relative benefits of non-parametric approaches). Specifically, we employed threshold free cluster enhancement (TFCE; Smith and Nichols, 2009) to identify significant voxels in each contrast. This approach is more conservative and effective at controlling type 1 errors than cluster-wise correction methods, producing voxel-wise outputs that enhance "cluster-like" structures.

Each contrast was tested via both whole brain correction and small volume correction (SVC). Our SVC used three small volume masks based on meta-analyses of neural responses to facial attractiveness (Mende-Siedlecki et al., 2013). This meta-analysis indicated three primary regions of interest in which target facial attractiveness led to greater activity than target trustworthiness across several studies. The regions include the anterior cingulate cortex (ACC; 0, 36, 6), portions of medial prefrontal cortex (mPFC; 4, 44, −6), and left striatum specifically caudate and nucleus accumbens (NAcc; −8, 14, −8). We constructed three masks for ACC, mPFC, and left striate using the Harvard-Oxford cortical structural atlas and the Harvard-Oxford subcortical structural atlas. The ACC mask included all voxels (1807 voxels) identified as at least 50% likely to reside in the cingulate gyrus, anterior division. We included ventral paracingulate and medial prefrontal cortex from the Harvard-Oxford cortical structural atlas in the mPFC mask. This was driven by the peak mPFC coordinates (4, 44, −6) from Mende-Siedlecki et al. (2013) falling outside and dorsally to the mPFC, as defined by the Harvard-Oxford Cortical Structural Atlas, in the ventral paracingulate gyrus. The mPFC mask included all voxels (981 voxels) 50% likely to reside in paracingulate gyrus and frontal medial cortex between MNI z-coordinates −20 and 4. The left striate mask included all voxels (533 voxels) at least 50% likely to reside in the left caudate or NAcc.

Secondary fMRI Analyses

Additional exploratory analyses were conducted on BOLD response during video watching. For these analyses the processing stream proceeded the same as for the face images, with first level contrast of love video – self-expansion video, love video – neutral video, self-expansion video – love video, self-expansion video – neutral video, neutral video – love video, and neutral video – self-expansion video.

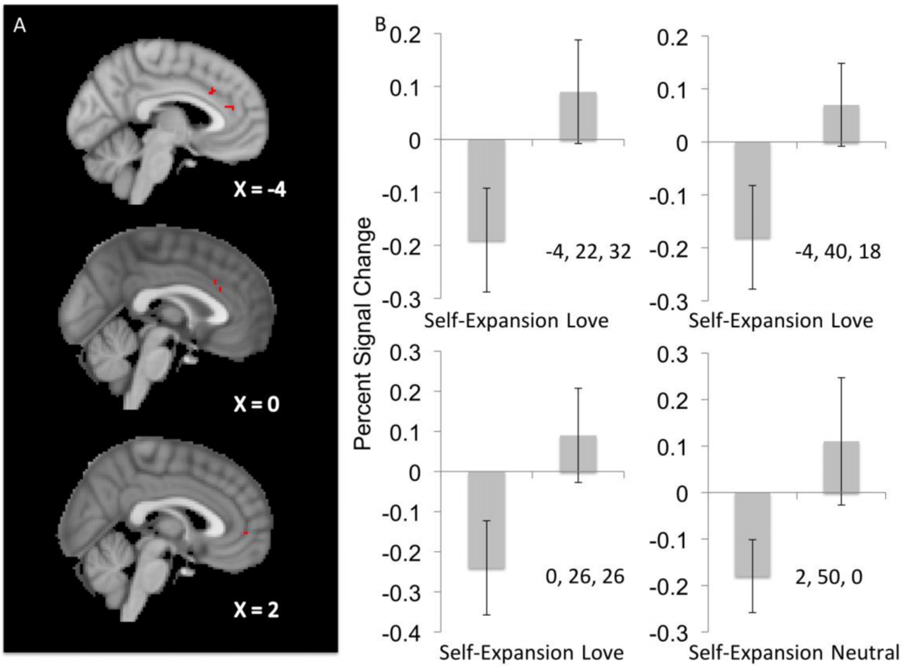

FIGURE 3 | (A) Displays sagittal slices with the locations of significant clusters of activity in the Love-Self-Expansion contrast (top two slices) and Neutral-Self-Expansion contrast (bottom slice) during opposite sex face perception (relative to same sex face perception). **(B)** Shows four bar graphs of mean percent signal change, with 95% confidence intervals, in the relevant prime conditions (i.e. Self-Expansion and Love or Self-Expansion and Neutral) during opposite sex face perception (relative to same sex face perception). MNI coordinates are placed in the lower right quadrant of each graph to indicate the ROI being displayed.

Meta-Analysis Based ROI Analyses

To further substantiate the small volume corrected analysis, we also created 9 mm^3 masks around each peak voxel identified as responding to facial attractiveness more than trustworthiness in Mende-Siedlecki et al. (2013) meta-analysis (i.e. ACC; 0, 36, 6; mPFC; 4, 44, −6; and NAcc; −8, 14, −8). This involved getting the mean percent signal change from all voxels within each mask for the opposite sex minus same sex face contrast and conducting one-tailed paired-samples *t*-tests on the comparison between each of the three conditions within each ROI. Based on theory and findings regarding derogation of alternatives, we predicted lower BOLD response in the self-expansion condition relative to both the love and neutral conditions in all three ROIs, and lower BOLD response in the love condition relative to the neutral condition. These analyses were conducted in JASP (JASP Team, 2019).

RESULTS

Main Effects of Prime Condition

No significant main effects in the focal contrasts were detected in the whole brain corrected analysis. Small volume correction revealed main effects in the ACC and mPFC in the love prime minus self-expansion and neutral prime minus self-expansion conditions. No significant effects were found in any other contrast: self-expansion minus love, self-expansion minus neutral, neutral minus love, or love minus neutral.

TABLE 1 | Significant clusters of activity for the main effects of prime on perception of opposite sex vs. same sex faces.

Structural location	Number of voxels	*Z*-max	*X*	*Y*	*Z*
Love – self expansion					
dACC	12	3.42	−4	22	32
dACC	5	3.77	−4	40	18
dACC	3	3.26	0	26	26
Neutral – self-expansion					
mPFC	4	3.75	2	50	0

Love Prime Minus Self-Expansion Prime Contrast

Three significant clusters of activity were detected in ACC indicating increased activity to opposite sex faces relative to same sex faces after a romantic love prime relative to after a self-expansion prime. The largest cluster (ACC1; −4, 22, 32) peaked most dorsally relative to the smallest cluster (ACC3; 0, 26, 25), which was dorsal to the middle cluster (ACC2; −4, 40, 18). Follow up analyses indicate that whereas ACC was more active to opposite sex attractive faces after the love prime, it was less active following the self-expansion prime (see **Figure 3** and **Table 1** for primary results, and **Table 2** for estimates of effect size and effect size 95% confidence intervals for each contrast).

Neutral Prime Minus Self-Expansion Prime

Activity to opposite sex faces relative to same sex faces was also diminished after the self-expansion prime relative to the

TABLE 2 | Cohen's *d* and 95% confidence intervals for each contrast exploring the main effects of prime on perception of opposite sex vs. same sex faces within each functional region of interest.

ROI	Contrast	Cohen's *d*	95% CI of Cohen's *d*	
			Lower bound	Upper bound
dACC1	Self-expansion – love	−0.792	−1.315	−0.251
	Self-expansion – neutral	−0.663	−1.167	−0.143
	Love – neutral	0.1	−0.364	0.562
dACC2	Self-expansion – love	−0.861	−1.396	−0.308
	Self-expansion – neutral	−0.452	−0.932	0.04
	Love – neutral	0.162	−0.306	0.624
dACC3	Self-expansion – love	−0.767	−1.286	−0.23
	Self-expansion – neutral	−0.495	−0.979	0.002
	Love – neutral	0.148	−0.319	0.61
mPFC	Self-expansion – love	−0.489	−0.973	0.007
	Self-expansion – neutral	−0.875	−1.412	−0.319
	Love – neutral	−0.078	−0.54	0.386

neutral prime in the mPFC (2, 50, 0). Similar to the effect of self-expansion in ACC it appears that mPFC responses to faces were decreased as a function of the self-expansion prime, whereas they were increased in the neutral condition.

Meta-Analysis Based ROI Analysis Results

To supplement the small volume corrected analyses, we also conducted analyses on mean percent signal change in each condition extracted from 9 mm^3 masks focused on the peak coordinates from Mende-Siedlecki et al. (2013). Given that these coordinates were derived independently from the data, this approach strengthens our interpretation if it provides agreement with SVC analyses. All analyses were one-tailed paired samples *t*-tests. Because each of these regions of interest are associated specifically with increased responses to attractive faces, this approach provides a relatively strong test of the specific hypotheses that self-expansion and love may lead to derogation of alternatives by focusing on attraction sensitive neural activity.

In the mPFC ROI, mean percent signal change in the self-expansion condition ($M = -0.098$, SE = 3.85) was not significantly less than in the love condition ($M = -0.534$, SE = 4.82), $t(17) = -1.344$, $p = 0.098$, $d = -0.317$, nor was percent signal change lower in the love condition than in the neutral condition ($M = 1.45$, SE = 2.75), $t(17) = -0.249$, $p = 0.403$, $d = -0.059$. There was a significantly less percent signal change in the self-expansion condition relative to the neutral condition, $t(17) = -2.054$, $p = 0.028$, $d = -0.484$. This indicates less neural activity to attractive opposite sex faces in a region associated with responding to attractive faces after the self-expansion manipulation when compared to a neutral condition, supporting one of the primary hypotheses in this ROI.

In the ACC ROI, mean percent signal change in the self-expansion condition ($M = -7.64$, SE = 2.43) was significantly less than in the love condition ($M = 2.70$, SE = 3.98), $t(17) = -2.264$, $p = 0.018$, $d = -0.534$. There was also significantly less percent signal change in the self-expansion condition relative to the neutral condition ($M = 1.18$, SE = 4.00), $t(17) = -1.819$, $p = 0.043$, $d = -0.429$. This indicates less neural activity to attractive opposite sex faces in a region associated with responding to attractive faces after the self-expansion manipulation when compared to a neutral. Percent signal change was not significantly lower in the love condition relative to the neutral condition, $t(17) = -0.242$, $p = 0.594$, $d = 0.057$.

In the NAcc ROI, mean percent signal change in the self-expansion condition ($M = -3.35$, SE = 2.75) was not significantly different than in the love condition ($M = 2.18$, SE = 2.75), $t(17) = -1.111$, $p = 0.141$, $d = -0.262$, and not significantly different than in the neutral condition ($M = -0.142$, SE = 3.09), $t(17) = -0.934$, $p = 0.182$, $d = -0.220$. Percent signal change was also not significantly lower in the love condition than in the neutral condition, $t(17) = 0.423$, $p = 0.661$, $d = -0.100$.

Correlations With Inclusion of Other in the Self

Correlations between IOS and neural response in ACC ROIs indicated a significant negative correlation between IOS and percent signal change in the opposite sex face minus same-sex face contrast in the self-expansion prime condition, ACC1, $r(18) = -0.68$, $p = 0.002$, ACC3 $r(18) = -0.50$, $p = 0.037$, indicating that those who reported greater inclusion of their partner in the self during the scanning session also had decreased ACC neural response to opposite sex faces (relative to same sex faces) during the self-expansion condition (see **Figure 4**). No significant correlations were found for the love condition, nor for the neutral condition.

Secondary Analyses

Blood oxygenation level dependent response during presentation of the different video types was contrasted across all possible paired comparisons. We found regions of enhanced activation to the love videos relative to both the neutral and self-expansion videos. We also found regions of enhanced activation to the neutral video relative to the love video. No significant effects emerged in the other contrasts: neutral minus self-expansion, self-expansion minus love, and self-expansion minus neutral.

Love Minus Neutral Video

Several significant clusters of activity indicated regions in which activity was greater during the love video relative to the neutral video. Clusters peaked in the medial frontal pole, bilateral superior temporal gyrus, right thalamus, occipital cortex, hippocampal, parahippocampal, and temporal fusiform regions. These activations are consistent with heightened visual attention to social stimuli, indicating that the love videos may have enhanced activity in networks associated with social perception processes (see **Table 3** for coordinate and cluster details).

Love Minus Self-Expansion Video

Two significant clusters of activity indicated regions in which activity was greater during the love video relative to the self-expansion video. Both clusters peaked in occipital cortex

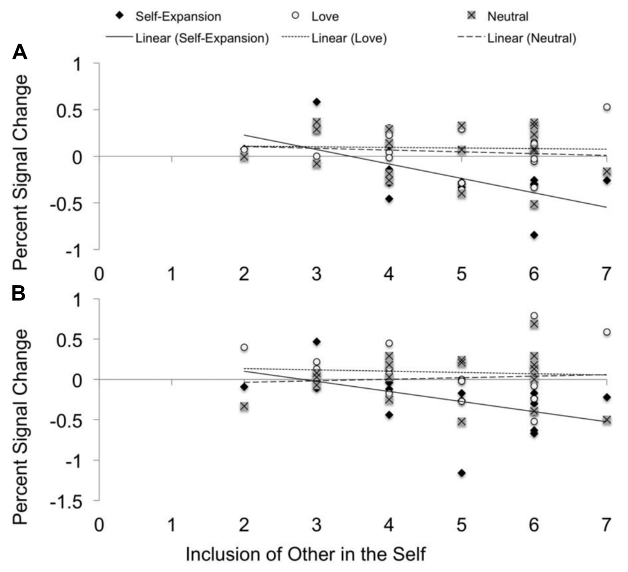

FIGURE 4 | Each scatterplot shows the correlation between percent signal change in each prime condition during opposite sex face perception (relative to same sex face perception) and self-report of relationship closeness using the IOS. The self-expansion condition is indicated by diamonds and an unbroken fit line, the love condition is indicated by circles with a dotted fit line, and the neutral condition is indicated by boxed x's and a dashed fit line. Scatterplot **(A)** includes the average percent signal change across all voxels in the dACC cluster peaking at MNI coordinates –4, 22, 32. Scatterplot **(B)** includes the average percent signal change across all voxels in the dACC cluster peaking at MNI coordinates 0, 26, 26.

TABLE 3 | Significant clusters of activity for the main effects of video type.

Structural location	Voxels	*Z*-max	*X*	*Y*	*Z*
Love minus neutral					
Medial frontal pole	848	5.18	0	64	2
Sup. temporal gyrus	780	5.73	−56	−14	−4
Sup. temporal gyrus	363	4.66	50	−2	−22
Thalamus	85	5.29	2	−6	6
Occipital pole	84	4.82	2	−90	0
Putamen	33	4.2	−20	16	−4
Parahippocampal	12	5.73	−16	−26	−12
Occitpital pole	8	5.25	−26	−98	−2
Temporal fusiform	8	4.44	40	−10	−24
Occitpital pole	4	4.5	28	−98	−10
Hippocampus	3	5.24	−38	−20	−12
Love minus self-expansion					
Sup. occipital	2	6.91	−36	−74	56
Sup. occipital	1	6.67	−34	−78	54
Neutral minus love					
Posterior cingulate	4	6.86	6	−26	22
Posterior cingulate	1	7.01	−6	−30	20

reinforcing the possibility that visual attention was heightened during the love videos (see **Table 3**).

Neutral Minus Love Video

Two significant clusters of activity indicated regions in which activity was greater during the neutral video relative to the love video. Both clusters peaked in the posterior cingulate cortex. This may indicate greater default mode network activity during the neutral video, indicating increased internal attention (see **Table 3**).

EXPERIMENT 2 DISCUSSION

We found neural activity in regions associated with perceiving attractive faces of the opposite sex to be diminished in the self-expansion condition relative to the romantic love and neutral conditions. This diminished activity was detected in both anterior cingulate and medial prefrontal cortices. The anterior cingulate is a core hub in the salience network (Sridharan et al., 2008), which involves switching from internal attention to external attention. This network is commonly activated by emotionally evocative stimuli, surprising events, cognitive errors, and other occurrences that require the focusing of executive resources and attention on the current context. It is unsurprising that viewing an attractive member of one's preferred sex would activate this network given its role in processing of motivationally significant stimuli. The medial prefrontal cortex is frequently involved in processing emotional information and reward, and is part of the ventral dopamine pathway (Berridge, 2012) that signals incentive salience, or "wanting". The subsection of the mPFC found in this study is associated with both affective and decision making processes (de la Vega et al., 2016), and may be critical for using affective information in the service of decision making and other cognitive functions.

The modulation of the aforementioned regions suggests that priming for self-expansion may lead to reduced interest in alternatives by diminishing the perceived attractiveness of potential alternatives. Participants who reported greater IOS after the self-expansion manipulation also had decreased attraction-correlated neural response to opposite sex faces (relative to same sex faces). Each of these findings support the hypothesis that self-expansion might promote derogation of alternatives by altering the incentive salience of alternative faces. Notably, the differences in activity were primarily found in medial prefrontal regions strongly associated with reward processing generally, and interpersonal attraction specifically. Whereas it is possible that these differences are driven by attentional factors, the primary impact of self-expansion on attraction to alternatives seems to occur in regions more strongly associated with motivation and evaluation. Furthermore, this is the first time to our knowledge that this novel procedure to manipulate self-expansion has been used in research.

There are important caveats to these conclusions. First the main effects of prime type on the neural response to attractive opposite sex faces were not robust to whole brain corrections. This likely indicates that the current study is somewhat underpowered and increases the probability that the findings are a type I error. This concern is somewhat mitigated by the use of data independent ROI analyses, and data independent correlations between inclusion of other in the self (an indicator of previous relationship based self-expansion) and activity in the ROIs, but not sufficiently that readers should come away certain that the effects will replicate. Future studies should replicate this finding with larger samples to verify and extend the current findings. Second, although we selectively looked in regions that are well demonstrated to respond to the perception of attractive faces, these regions are also active in many other kinds of contexts and respond to diverse stimuli. Therefore, given the known problems with reverse inference (Poldrack, 2006), such conclusions about what the neural response might mean should be taken with appropriate caution.

Notably, no differences were found between the romantic love and neutral conditions. Whereas previous research has shown behavioral evidence for diminished attention to alternatives in conditions enhancing feelings of romantic love, we found no evidence for diminished attention to alternatives in the love condition relative to the neutral condition. This may be due to methodological differences between the studies, slower memory consolidation processes that fMRI was unable to detect that led to the effects in behavioral studies, or due to inadequate power to detect any effects.

In addition to the primary findings, we also found differences in BOLD response to videos of different types. Love videos evoked greater BOLD response relative to neutral videos in large portions of the brain associated with the processing of social stimuli, such as the superior temporal lobe and medial prefrontal cortex. Additional activity indicated greater involvement of regions associated with long term memory in hippocampal and parahippocampal regions, heightened visual attention in the occipital cortex and fusiform gyrus, and subcortical regions associated with motivation and affect such as the putamen. Most of this heightened activity was not seen when compared to the self-expansion video. The only region with greater BOLD response during the love videos relative to the self-expansion videos included occipital cortex. These findings tentatively suggest that love videos induce greater psychological engagement relative to neutral videos, but only increase visual attention relative to self-expansion.

One potential for future research involves an investigation of how relational self-expansion may be linked to implicit (as measured by fMRI) evaluations of one's partner and implicit evaluations of alternatives. Perhaps the most promising future direction for research following up on these effects would include a way to overcome the reverse inference problem by identifying activity that is attraction specific. This may be possible with the right types of analytic methods and sufficient neuroimaging groundwork. For example, multivoxel pattern analysis has been successfully used to identify neural activity specifically associated with physical pain (Wager et al., 2013). If one could identify attraction specific activity, then one could apply similar methods used in this study to verify that the reductions in activity observed are specifically a function of diminished attraction to potential alternatives.

CONCLUSION

In conclusion, infidelity is a widespread phenomenon that can greatly affect the welfare of individuals, their partners, and families. And more generally the role of relationship alternatives is central to theories of relationship commitment. As suggested by the findings of Experiment 1, identifying circumstances under which different kinds of alternatives are seen as most desirable may be an important factor in helping individuals avoid the temptation of attractive alternatives. The self-expansion model represents a novel approach that may elucidate some of the factors that determine how strongly people cognitively process – and experience the pull of – attractive relationship alternatives.

Experiment 2 is tentatively suggestive that self-expansion primes promote derogation of alternative partners by reducing their perceived attractiveness directly, whereas romantic love primes do not. This reduction in attraction to alternatives appears to occur in the processing of attractiveness per se, not necessarily via decreased attention to the alternatives. This may be because the current relationship is bolstered by feelings of self-expansion diminishing the relative attractiveness and therefore the incentive salience of alternative partners.

These findings, as well as the methodological innovations, both Experiment 1 and Experiment 2, suggest promising future directions for applying the self-expansion model to research on infidelity and pair bonding. Whereas the importance of the findings themselves offer an initial glimpse into the causal effect of self-expansion on attraction to alternatives, the methodological innovation related to manipulating self-expansion may be even more important and should open up new avenues for future research.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Stony Brook IRB. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

IT collected the data, designed the study, analyzed the data, and wrote the manuscript. LB analyzed the data, wrote the manuscript, and interpreted of the fMRI data. AA analyzed the data, wrote the manuscript, and designed the study.

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REVIEW
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What's in a Moment: What Can Be Learned About Pair Bonding From Studying Moment-To-Moment Behavioral Synchrony Between Partners?

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Our understanding of the behavioral and physiological mechanisms of monogamy largely comes from studies of behavioral interactions unique to pair-bonded individuals. By focusing on these highly marked behaviors, a remarkable conservation in the mechanisms underlying pair bonding has been revealed; however, we continue to know very little about the range of behavioral and neurobiological mechanisms that could explain the great diversity of pair-bonding phenotypes that exists both within and across species. In order to capture the dynamic nature of bonds over time and across contexts, we need specific, operationally-defined behavioral variables relevant across such a diversity of scenarios. Additionally, we need to be able to situate these behavioral variables within broader frameworks that allow us to interpret and compare patterns seen across species. Here I review what is known about behavioral synchrony with respect to pair bonding and discuss using synchrony as such a variable as well as a framework to expand on our understanding of pair bonding across timescales, contexts and species. First, I discuss the importance of behavioral synchrony and parental coordination for reproductive success in monogamous biparental bird species. Second, I highlight research documenting the critical importance of interpersonal coordination for human social relationships. Finally, I present recent work that experimentally bridges these lines of research by quantifying moment-to-moment behavioral synchrony during brief social interactions in zebra finch dyads. All together, these distinct perspectives support the notion that synchrony (1) is a shared premise for sociality across species, (2) is deeply shaped by social experiences, and (3) exists across timescales, behaviors, and levels of physiology. Conceptualizing pair bonding through the framework of behavioral synchrony is likely to facilitate a deeper understanding of the nuances of how social experiences and interactions impact the brain and behavior.

Keywords: synchrony, coordination, calls, parent, couple, nest

INTRODUCTION

Monogamy and Pair Bonding

The word *monogamy* permeates scientific and popular literature on animals, including humans (Wundt, 1894; Wickler and Seibt, 1981; Dewsbury, 1988). Monogamy is found across species. While it is relatively rare in mammals (4–5%) (Kleiman, 1977), it is more common in primates (∼15%) (Díaz-Muñoz and Bales, 2016) and is the dominant breeding strategy in birds (∼90%) (Lack, 1968; Silver, 1983; Silver et al., 1985). Monogamy is also found in insects (Nalepa and Jones, 1991; Jaffé et al., 2014), lizards (Bull, 2000), and fish (Andrew DeWoody et al., 2000; Morley and Balshine, 2002; Whiteman and Côté, 2004). Traditionally the term monogamy has been used to refer to an "absolute commitment" between a male and female: the male and female breed exclusively with each other, both participate in parental care, remain completely committed social partners, and benefit from reduced sexual conflict (Wundt, 1894; Wickler and Seibt, 1981; Dewsbury, 1988). This monogamous partnership between a male and female is referred to as a pair bond. However, monogamy as a reproductive strategy has resulted from various evolutionary trajectories and is correspondingly diverse; thus, our understanding of monogamy is continually being re-evaluated and developed (Gowaty, 1996; Reichard, 2003; Reichard and Boesch, 2003; Lukas and Clutton-Brock, 2013; Díaz-Muñoz and Bales, 2016; Tecot et al., 2016).

Many of the behavioral interactions between monogamous partners are highly marked, pair-specific expressions of affiliation seemingly resulting from, and reserved for, a pair bond. These highly marked, exclusive pair-directed interactions may be obvious during courtship and initial pair bond formation (Wachtmeister, 2001; Soma and Garamszegi, 2015; Manica et al., 2016; Ota et al., 2018) as well as during the coordination of parental duties (Mariette, 2019). Additionally, for territorial or non-gregarious species the monogamous partnership may be the primary affiliative relationship. For example, selective affiliation for a mate and increased aggression toward novel opposite-sex individuals is used to classify the presence/absence of a pair bond in prairie voles (*Microtus ochrogaster*) (Williams et al., 1992; Resendez et al., 2016). The vast majority of research on the behavioral and physiological mechanisms of pair bonding has taken advantage of these highly-marked examples of monogamy, and this approach has successfully revealed remarkable conservation of key behavioral and neurobiological mechanisms of pair bonding across species. These behavioral and neural mechanisms have been foundational for our understanding of pair bonding across taxa (reviewed in Young and Wang, 2004; O'Connell and Hofmann, 2012; Donaldson and Young, 2016).

Our ever-expanding understanding of the complexity of pair bonding is evident from the changing definition of monogamy itself. Traditionally, monogamy was used to describe partnerships in which individuals have a single, exclusive sexual partner, referred to as genetic monogamy (Wundt, 1894; Wickler and Seibt, 1981; Dewsbury, 1988). However, we now know that genetic monogamy is rare: both within and across breeding periods males and females employ flexible mating strategies (Reichard, 2003; Díaz-Muñoz and Bales, 2016). Indeed, the vast majority of monogamous species are serially (sequentially) socially monogamous, having a single partner at a time, but multiple partners over a lifetime (Wickler and Seibt, 1981; Reichard, 2003). For example, humans may be classified as serially monogamous (Mulder, 2009), and most songbird species form new, transient bonds with each subsequent breeding season (Ens et al., 1996). Even within a breeding season, it is common for both males and females to participate in extra-pair courtship. While the pervasiveness of extra-pair mating was discovered in songbirds, it is also seen in mammals, including the prairie vole (Solomon et al., 2004; Ophir et al., 2008) and several species of primates (Díaz-Muñoz and Bales, 2016). Today, the term monogamy is predominately used to describe cases where a male and female cohabit, referred to as social monogamy (Black and Hulme, 1996; Reichard, 2003).

Research on both the behavioral and neurobiological underpinnings of monogamy has contributed to our understanding of the great diversity in pair bond phenotypes. There is growing evidence that the neurobiological mechanisms supporting pair bonds change over time, particularly between formation and maintenance (Aragona et al., 2006; Prior and Soma, 2015; Resendez et al., 2016; Scribner et al., 2019). More broadly, the neurobiology of social bonds also varies by relationship type (Beery et al., 2008, 2009, 2018). Behaviorally, both within and across species, pair bonds vary in many dimensions including duration and apparent strength of the bond (Black and Hulme, 1996; Tecot et al., 2016). Additionally, although biparental care is typically associated with monogamous mating systems, it is neither ubiquitous nor uniform. For species that do display biparental care, there is significant variation in how parental duties are shared between the male and female (Clutton-Brock, 1991; Hughes, 1998; Cockburn, 2006). Given the tremendous diversity in monogamy, it has even been argued that the term social monogamy is too general, capturing too many distinct phenotypes to be useful (Tecot et al., 2016). Considering the remarkable variability in monogamy within and across species, it stands to reason that highly marked behavioral interactions of pair bonds only represent a small subset of bonds and contexts. In other words, while we have a clear sense of the shared biological basis of pair bonding, we know very little about the behavioral and neurobiological mechanisms underlying the full range of social bonds and diversity in pair bonding phenotypes.

Challenges in Studying Pair Bonding

There are many challenges when it comes to extending our understanding of monogamy to encompass the diversity that exists across pair bonds. One challenge is that many of the highly marked behavioral variables described above are not applicable across species or contexts. An example of this problem across species can be demonstrated by attempting to apply behavioral variables from certain key model systems to other systems. For example, partner preference is a widely used behavioral metric for identifying monogamously bonded pairs; however, partner preference is not a clear indicator of pair bonds in all species (Prior et al., 2013). Rather, selective affiliation may be specific to modality and context (Gill et al., 2015; Fernandez et al., 2017). Even within a species, marked courtship displays are often absent, rare, or dramatically reduced in intensity after initial pair bonding. In other cases, the specific affiliative behaviors that are necessary for the formation of pair bonds may not be necessary for the maintenance of those bonds (Tomaszycki and Adkins-Regan, 2005, 2006). Overall, it has been particularly challenging to identify changes in affiliative behavior following the formation of a pair bond (Williams et al., 1992; Carter, 1998; Resendez et al., 2016; Scribner et al., 2019). Current research on pair-bond maintenance often requires interrogation of relatively subtle behavioral dynamics (Prior et al., 2016, 2019; Scribner et al., 2019).

A second challenge is how to disentangle the role of parental behavior and biparental care from pair bonding. As indicated above, the extent to which parental duties are shared varies both within and across species. Furthermore, for species that form and actively maintain life-long pair bonds, pair-directed behavior during breeding periods and non-breeding periods can be quite different (Black and Hulme, 1996), thus it is unclear how to compare pair bonds between breeding and non-breeding periods. Not only is this another case in which highly marked behavioral interactions may not be relevant across species and contexts, but this confound raises another set of challenges. First, across species, reproductive behaviors occur under specific neuroendocrine states, during which hormones have profound effects on brain and behavior in order to orchestrate breeding behavior and physiology. This observation raises the question of whether there are distinct neurobiological mechanisms underlying pair-directed behavior during breeding and non-breeding periods. Conversely, it is also important to know how the neuroendocrine conditions associated with breeding impact the expression of the behavioral metrics associated with pair bonding (Prior and Soma, 2015). Furthermore, the confound of biparental care raises questions about how we conceptualize a successful, or strongly bonded, partnership. From an evolutionary perspective, monogamy is a breeding strategy, and evaluation of monogamous partnerships requires assessment of an individual's reproductive success. There is evidence, however, that for monogamous species reproductive success is related to behavioral, not genetic, compatibility between partners (Ihle et al., 2015), and for species that form long-term pair bonds, reproductive success increases with time (Griggio and Hoi, 2011). This highlights the importance of assessing reproductive success across an individuals' lifespan and raises the question of how a pair's experience outside of breeding cycles impacts reproductive success.

A third challenge comes from the fact that not all pair-directed affiliative behaviors are equal. This is true both with respect to the functional significance of affiliative behaviors for a pair bond as well as the value of a behavioral metric of pair bonding for researchers. For example, the same affiliative behaviors used to assess the strength or quality of a bond are also often used to identify the presence of a pair bond initially. By this reasoning, it may be assumed that strongly bonded pairs display more affiliative behaviors across domains. However, various disruptions (e.g., brief stressors, pharmacological and hormonal manipulations) often affect one type of affiliative behavior and not another (Prior et al., 2014), or affect different types of behaviors in opposing ways (Prior et al., 2016, 2018). Such experiments raise the question of how different behavioral components contribute to the formation and maintenance of pair bonds as well as how to assess the consequences of such perturbations on pair bonds. Indeed, there is evidence that certain pair-directed behaviors may be more important for monogamous partnerships [e.g., allopreening (Kenny et al., 2017)].

In order to address these three challenges, we need to identify meaningful dependent variables that can be used to assess the dynamic nature of bonds over time and across contexts (both during breeding and non-breeding periods) and that can support comparisons across species. Because pair bonding fundamentally requires individuals to respond to and align with each other's behavior, I have turned to behavioral coordination or synchrony as a fundamental behavioral "unit" necessary for understanding social bonding. Behavioral synchrony has specific operational definitions that may be applied across types of affiliative behaviors, timescales, and social contexts. More broadly, behavioral synchrony could be applied as a framework with which to interpret changes or differences in subtle aspects of pair-directed affiliation. Importantly, although behavioral synchrony has been studied across taxa, including insects, fish, birds, and mammals (Bernieri and Rosenthal, 1991; Feldman, 2012b; Duranton and Gaunet, 2016), research on behavioral synchrony is faced with its own set of challenges. Understanding the challenges associated with studying behavioral synchrony itself is necessary in order to determine how behavioral synchrony may be used as a variable to deepen our understanding of pair bonding.

A NOTE ON METHODS: BEHAVIORAL SYNCHRONY

Behavioral coordination is inextricably linked with sociality, and synchrony is a ubiquitous component of that coordination. Behavioral coordination/synchrony is essential for a wide range of behaviors including: schooling/flocking (Boinski and Garber, 2000; Greenberg, 2001), group living (Conradt and Roper, 2005; Focardi and Pecchioli, 2005), hunting (Handegard et al., 2012; Bailey et al., 2013), and heterospecific communication [reviewed in Duranton and Gaunet (2016)]. In general it is clear that behavioral synchrony promotes social cohesion (Pays et al., 2007; King and Cowlishaw, 2009), affiliation (Sakai et al., 2010), and prosocial behavior (Van Baaren et al., 2004; Ashton–James et al., 2007; Gueguen et al., 2009) (reviewed in Duranton and Gaunet, 2016). One of the most significant challenges exists in operationalizing synchrony or coordination.

Here I use the term *behavioral synchrony* broadly to encompass the temporal and/or spatial coordination of behaviors as well as physiological and biological states during social interactions. In ethology, it has been proposed that behavioral synchrony has multiple components, including local synchrony (being in the same place at the same time), temporal synchrony (switching actions at the same time), and allelomimicry (engaging in the same behavior at the same time) [reviewed in Duranton and Gaunet (2016)]. In human research, the terms *interpersonal coordination* or *motor-sensory interpersonal synchrony* (individuals moving together and receiving the same sensory stimulation at the same time) are used to capture the integrated nature of bio-behavioral coordination (Bernieri and Rosenthal, 1991; Rennung and Göritz, 2016). Importantly behavioral synchrony is not limited to two individuals (dyads). For example, it is critical for understanding group dynamics such as schooling/flocking (Boinski and Garber, 2000; Greenberg, 2001) and colony living (Conradt and Roper, 2005; Focardi and Pecchioli, 2005). However, for the purpose of this review, I focus on research that investigates behavioral synchrony in social dyads. Furthermore, as a fundamental component of social behavior, many lines of research across disciplines are relevant to investigations of behavioral synchrony. This focus is particularly relevant for animal behavior research, where the terms behavioral synchrony and coordination are less pervasive than in human research. For example, spatial proximity or coordinated activities, which are commonly used dependent variables (Prior et al., 2014, 2016, 2018; Prior and Soma, 2015), are not referred to in the literature as measures of synchrony, despite that they would be classified as synchrony by the above definitions. Considered generally, spatial proximity itself is a hallmark of pair bonding and social bonding in birds and other species (Black and Hulme, 1996; Frigerio et al., 2001; Emery Thompson, 2019; Szipl et al., 2019); but such research lines are not included here.

Furthermore, given that behavioral synchrony promotes social cohesion (Pays et al., 2007; King and Cowlishaw, 2009), affiliation (Sakai et al., 2010), and prosocial behavior (Van Baaren et al., 2004; Ashton–James et al., 2007; Gueguen et al., 2009), it is easy to assume that behavioral synchrony must be positively correlated with pair bonding. Certainly the importance of synchrony in terms of temporal alignment and turn-taking is evident in highly marked behavioral interactions associated with monogamy such as vocal duetting (Hall and Magrath, 2007; Hall, 2009; Odom and Omland, 2017), courtship (Ota et al., 2015) and territorial displays (Ręk and Wong, 2017). However, in many cases these behavioral interactions are specific to key contexts, again leaving it unclear whether this type of coordination is important to pair bonds more generally. Additionally, increased coordination during these marked interactions may not afford any advantage to the partnership (Takeda et al., 2018). In fact, there has been very little research interrogating the relationship between behavioral coordination and pair bonding. At this time there is no clear evidence that behavioral synchrony is specialized or enhanced in monogamous partnerships, and it remains unclear whether synchrony is important for the formation and maintenance of pair bonds or whether variation in the pattern or extent of synchrony is of consequence for monogamous partnerships.

I situate this review within two extensive bodies of work illustrating the importance of moment-to-moment synchrony for monogamous partnerships. First, drawing from rich lines of work in behavioral ecology, I introduce evidence that behavioral synchrony "scales up." More specifically, I describe the phenomenon that the coordination of parental duties (over the course of hours to days) is achieved during subtle behaviors within brief social interactions. This "active negotiation" of parental duties introduces the notion of behavioral synchrony, alignment, and coordination during brief moments as a type of information exchange. Additionally, I work to address the challenges raised above regarding the confounds that result from focusing on monogamous partnerships during breeding periods. Second, I discuss the extensive literature from human research across the fields of psychology, sociology and anthropology, that have worked to operationalize interpersonal coordination during brief social interactions. This research elegantly integrates and extends the concept of synchrony beyond the behavior of individuals to peripheral physiology and neurobiology. Additionally, this work introduces the importance of our ability to perceive synchrony. In humans, we have a remarkable intrinsic capacity to assess interpersonal coordination of others and the consequences of interpersonal synchrony. Third, I present some of my recent work aimed at experimentally bridging these perspectives from behavioral ecology and social psychology. This work demonstrates the role of sex, social context and social experience in behavioral synchrony by quantifying moment-to-moment behavioral synchrony during brief social interactions in songbird (zebra finch) dyads (Prior et al., 2019, 2020).

Combined, these three areas of research highlight that behavioral synchrony (1) is a shared premise for sociality across species, (2) is deeply shaped by social experience and (3) can be assessed across timescales and behavioral/physiological levels. Importantly, while there is abundant evidence supporting the notion that behavioral synchrony is a fundamental component of monogamous partnerships, there is little evidence that behavioral synchrony is unique to, specialized for, or enhanced in monogamous partnerships. I discuss the significance of this apparent incongruity in the general discussion at the end of the manuscript.

BEHAVIORAL COORDINATION AND BIPARENTAL CARE IN BIRDS

For the majority of monogamous bird species, the male and female partner share parental duties. However, both within and between species there is substantial variation in the extent to which parental duties are shared. Across many species, parental duties appear to be actively negotiated at the level of the pair. This active negotiation takes place during brief social interactions at the nest, both during incubation (temperature regulation) and nestling provisioning (feeding of chicks). These social interactions often involve dynamic vocal exchanges that are modulated by nesting phase, individual identity as well as by other factors (e.g., presence of a predator) (Mainwaring and Griffith, 2013; Mariette, 2019). The evidence suggesting that these brief social interactions are important for the coordination of parental duties comes from a range of avian species in which characteristics of these brief social interactions have been related to the coordination of parental duties and/or reproductive success of the pair.

There is substantial research from the fields of behavioral and evolutionary ecology on the function of parental coordination across many species of birds. Here, I summarize several of these lines of work, identifying: (1) how behavioral "coordination" or "synchrony" is operationally defined (during brief social interactions and during parental behavior); (2) the behavioral mechanisms (e.g., characteristics of the brief social interactions) that are thought to be involved in the active negotiation of behavioral coordination; and (3) how behavioral measures of coordination have been related to measures of reproductive success or pair bond success. Given the variation in parental behavior across species and by reproductive stage, I summarize these lines of work separately for incubation and provisioning of chicks. Additionally, I work to highlight the species-specific ecologies that influence patterns of parental coordination, the mechanisms by which parental duties are coordinated, and the consequences of parental coordination.

Incubation

The primary goal of parental care during incubation is to control the thermal environment of the eggs. In many species, the female predominately incubates the eggs whereas in others the parents divide incubation duties equally. In species where the male does not incubate, he may perform other duties such as provisioning the female and/or acting as a sentinel and alerting the female to nest predators.

Some of the earliest evidence demonstrating that monogamous partners are actively negotiating and coordinating parental care duties came from research on ring doves (*Streptopelia risoria*). Female ring doves do the majority of the incubation, whereas males typically contribute incubation relief during the day. The extent of this incubation relief varies greatly from pair to pair as males have been observed to incubate 23–76% of the time (Wallman et al., 1979). This sharing of parental duties is a pair-level phenotype, not entirely driven by the male or female: the proportion of time each partner incubates changes when they are re-paired with a different mate during a new breeding cycle (Wallman et al., 1979). The majority of these incubation exchanges (over three quarters) are coordinated, meaning they are initiated by the incubating parent and leave no gap in incubation (Ball and Silver, 1983; Silver et al., 1985). The most common behavioral exchange associated with this coordinated transition is a brief allopreening bout (almost half of exchanges) (Ball and Silver, 1983). This coordination between partners does not appear to be caused simply by physiological synchrony around the nesting cycle, because switching partners between nests at the same breeding point (thus in the same physiological condition) within a breeding season causes significant disruptions in the timing of incubation bouts, and changes patterns of parental interactions (Ball and Silver, 1983). This experimental evidence is consistent with the notion that the coordination of parental behavior is an emergent consequence of the behavioral interactions between partners.

Female great tits (*Parus major*) also are directly responsible for much of the parental care: they build the nests, incubate the eggs, and brood hatchlings largely alone (Cramp and Perrins, 1982). Male great tits contribute to parental care by provisioning the female with food while she incubates (Hinde, 1952). Interestingly, the male coordinates his provisioning behavior with the female. During this period, the male and female have brief vocal exchanges where the male sings from a perch and the female answers predominately with calls (Gorissen and Eens, 2004; Boucaud et al., 2016b,c). These vocal exchanges are longer and more rapid when the male feeds the female (Boucaud et al., 2016c), and experimentally manipulating food availability shows that females use calling as an honest indicator of their hunger levels (Boucaud et al., 2016b). These lines of work emphasize that much behaviorally relevant information can be communicated in these coordinated nesting exchanges.

Male and female zebra finches (*Taeniopygia guttata*) share incubation duties relatively equally. Again this sharing of duties is an active process which appears to be negotiated via calling exchanges (Elie et al., 2010; Boucaud et al., 2016a, 2017; Villain et al., 2016). These interactive vocal exchanges, similar to "duets," were originally described in wild breeding zebra finches (Elie et al., 2010). There are two main types of vocal exchanges, both of which can be initiated by either the male or female. "Meeting sequences" are the dominant vocal exchange during incubating, occurring when one partner returns to the nest, which may or may not result in a nesting exchange (or nesting relief). During "sentinel sequences" one partner is perched outside the nest and the pair has a brief vocal exchange, which seems to be related to shared vigilance and nesting defense (Elie et al., 2010; Mainwaring and Griffith, 2013). Both types of vocal sequences are very brief (1-2 minutes on average) and both types are characterized by tight temporal coordination and alternation of calling between partners (Elie et al., 2010). In wild zebra finch pairs it has been demonstrated that characteristics of these vocal exchanges predict whether or not a nest exchange (or relief) will occur; specifically, the female's call rate and the acoustic structure of her calls predicts whether or not the male performs a nesting relief (Boucaud et al., 2017). In captive zebra finches, the timing of incubation bouts has been experimentally manipulated via delaying the male partners' return to the nest, thus extending the female's incubation bout (Boucaud et al., 2016b). Interestingly, call rate and the acoustic structure of calls during the nesting relief following this disruption are significantly affected by the delay and predicts the duration of the female's subsequent time off the nest (Boucaud et al., 2016b). Together with the work in great tits, these lines of work emphasize the range of ways birds can coordinate activities using dynamic vocal exchanges at the nest.

Some species also vary in the proportion of pairs that form any type of monogamous partnership. The northern lapwing (*Vanellus vanellus*) is a biparental shorebird that forms monogamous partnerships about 80% of the time (Liker and Székely, 1999). The male's contribution to incubation is highly variable (Liker and Székely, 1999). Typically, incubation exchanges occur at "exchange gaps" and thus are not coordinated exchanges. Having exchange gaps during incubation is not uncommon among shore and seabirds (Niebuhr and McFarland, 1983; Bulla et al., 2013). Prior to departing from the nest, females, but not males, perform vocal displays which appear to signal the male. Female vocalizing increases the likelihood that the male will incubate and decreases the duration of the exchange gap (Sládeček et al., 2019). Despite significant species differences in how incubation duties are shared, the range of ways birds coordinate activities using dynamic vocal exchanges at the nest remains striking.

Provisioning Nestlings

Whereas there is significant variation in how incubation duties are shared, there is much greater consistency across species in biparental care around nestling provisioning. The coordination of nestling provisioning can be described in several ways. Parents can either alternate or synchronize the timing of their visits. Synchronization between parents occurs when both parents visit the nest at the same time (typically defined as entering the nest within 1–2 min of each other). This coordination is consistent broadly with the definition of activity synchrony (Duranton and Gaunet, 2016). Parents can also synchronize their foraging trips.

In the vast majority of species studied, parents synchronize a majority of their nest visits and alternate their feeding trips more than would be expected by chance [great tits (Johnstone et al., 2013); blackcap (*Sylvia atricapilla*) (Leniowski and Węgrzyn, 2018); zebra finches (Mariette and Griffith, 2012); dovekie (*Alle alle*) (Wojczulanis-Jakubas et al., 2018); long tailed tits (*Aegithalos caudatus*) (van Rooij and Griffith, 2013); rock sparrow (*Petronia petronia*) (Baldan and Griggio, 2019)]. As with the coordination of incubation bouts, the coordination of nestling provisioning seems to be an active process, and there are many potential fitness advantages of synchronized provisioning, such as decreasing risk of predation during active foraging and minimizing trips to the nest. Indeed, in great tits, it has been shown that parents may adjust their provisioning of chicks more in response to their partner than to the chicks' begging calls (Hinde and Kilner, 2006).

There are several lines of evidence suggesting that partner coordination improves reproductive success for the pair (Mariette and Griffith, 2012, 2015), minimizes reproductive conflict (Baldan and Griggio, 2019), and can even decrease sibling conflict (Shen et al., 2010). One clear explanation for this fitness advantage is that coordinated provisioning trips decrease the total number of nesting disturbances and thus decreases predation (Bebbington and Hatchwell, 2015). Partners may also benefit from the increased vigilance of their partners (Elie et al., 2010; Mainwaring and Griffith, 2013). For example, in the rock sparrow (*Petronia petronia*), biparental care is highly variable and typically one parent (usually the male) will desert the brood at some point prior to the fledging of chicks. Pairs that do not desert, but remain together, appear to be more synchronized (Baldan and Griggio, 2019). More specifically, partners that remain together have higher levels of alternation of nest visits during provisioning of chicks and increased synchronization of visits (Baldan and Griggio, 2019). However, the benefit of parental coordination is species-specific.

Physiological Mechanisms and Consequences of Behavioral Synchrony

There has been very little research investigating the physiological mechanisms underlying parental coordination or the reciprocal impact of parental coordination on an individual's brain and behavior. There is, however, considerable evidence that the coordination of reproductive physiologies is important (pairs need to be reproductively ready to breed at the same time), and in species that actively maintain life-long pair bonds the synchronization of yearly patterns in circulating hormone levels within a pair is associated with reproductive success. In graylag geese (*Anser anser)* and domestic geese (*Anser anser domesticus*), yearly patterns of circulating testosterone levels are correlated within a pair, and pairs with more coordinated patterns of circulating testosterone have greater reproductive success (Hirschenhauser et al., 1999, 2010; Hirschenhauser, 2012). Hirschenhauser (2012) proposed several possible explanations for this relationship. Pairs with higher testosterone coordination may be more coordinated in their reproductive physiology, and subsequently in their expression of appropriate hormonally-mediated behaviors. Alternatively, hormonal coordination could be a reflection of how behaviorally and hormonally responsive an individual is to their mate (Hirschenhauser, 2012). Thus, hormonal synchrony may be a cause or consequence of reproductive success. Furthermore, it is unclear whether it is important for biparental care or pair bonding *per se* (Hirschenhauser, 2012).

In a few species, reproductive success has also been linked to pair-level similarity in circulating glucocorticoid levels, although the relationship between the similarity in partner's glucocorticoid levels and reproductive success varies across species. In great tits, pairs with high reproductive success have similar baseline corticosterone levels (Ouyang et al., 2014); additionally, circulating corticosterone levels become more similar between pairs the longer they are together (Ouyang et al., 2014). Similarly, in barn owls (*Tyto alba*) reproductive success is higher for pairs that have greater similarity in baseline corticosterone levels during incubation, but a greater dissimilarity in stress-induced circulating corticosterone levels during provisioning of chicks (Béziers et al., 2019). However, for eastern bluebird (*Sialia sialis)* parents, similarity in hormone levels (within the pair) does not appear related to reproductive success; although, individual hormonal levels are related to the expression of male and female parental behavior (Burtka et al., 2016). Combined, even when hormonal similarity does relate to reproductive success, it is unclear how such hormonal alignment would afford pairs greater reproductive success.

At this point it would be purely speculative to say whether relationships between parental coordination and hormonal synchrony are a cause or consequence of behavioral synchrony during brief interactions. One potential strategy that may allow us to disentangle behavioral synchrony (during brief interactions), parental coordination, and hormonal synchrony is to expose pairs to perturbations, disrupting levels of coordination between partners. In general behavioral disruptions are valuable in eliciting pair-directed behavior (Prior et al., 2014, 2016), and disrupting parental coordination has been effectively used to clarify the behavioral mechanisms underlying parental coordination (Boucaud et al., 2016a,b, 2017).

Summary

Together these lines of work highlight the extent to which behavioral coordination between partners may be critical for biparental care in many species. The research presented above nicely operationalizes parental coordination over larger timescales. While many lines of evidence suggest that the benefit of parental coordination is a reduced predation risk, it is noteworthy that even in laboratory situations behavioral coordination between partners has been linked to improved reproductive success. For example, in the cockatiel (*Nymphicus hollandicus*), a gregarious Australian parrot, the coordination of activities prior to breeding was associated with improved fecundity during subsequent breeding periods (Spoon et al., 2006). Additionally, in the common marmoset (*Callithrix jacchus*), an individuals' contribution to parental care is associated with hormonal synchrony and relationship quality (Finkenwirth et al., 2015; Finkenwirth and Burkart, 2017, 2018). The fact that parental coordination clearly affords a fitness advantage suggests there may be strong selection pressures supporting behavioral synchrony, although this could be consistent with the notion that coordination is more related to the sharing of parental duties than to monogamy.

Importantly while this section has focused on birds, numerous studies across a range of species highlight that behavioral compatibility generally improves reproductive success [e.g., convict cichlid *Amatitlania siquia* (Laubu et al., 2016); mound-building mouse, *Mus spicilegus* (Rangassamy et al., 2015)]. In prairie voles, it is social rather than genetic monogamy that has been linked to increased reproductive success (Ophir et al., 2008). However, it is also important to note that the coordination of parental duties is not unique to monogamous systems. Cooperatively-breeding species also actively coordinate nestling provisioning, form family-bonds, and display hormonal synchrony (Raihani et al., 2010; Finkenwirth et al., 2015; Finkenwirth and Burkart, 2017, 2018; Savage et al., 2017). In colonial species, there is evidence that reproductive synchrony can promote affiliative relationships even outside of the pair bond (Brandl et al., 2019). The interrelationship between patterns of sociality, parental care, parental coordination, and moment-to-moment behavioral synchrony could be disentangled by comparing closely related bird species across a range of social ecologies and mating systems.

What is particularly striking from the behavioral ecology work on birds is the extent to which brief social interactions actively coordinate parental coordination on longer timescales. In other words, these systems support the notion that behavioral coordination "scales up." This is striking because behavioral synchronization does not require active communication and negotiation (Dostálková and Špinka, 2007). Many monogamous seabirds share incubation duties evenly (Black and Hulme, 1996) but there may be little room for such negotiation between partners in the timing of nest reliefs. In these species, the foraging partner waits to recover its body mass before returning to relieve the incubating partner, despite the fact that a delayed return may cause the incubating partner to abandon the nest (Davis, 1982; Chaurand and Weimerskirch, 1994; Yorio and Boersma, 1994). However, if we consider the number of bird species with nest-specific vocal displays [red-winged blackbirds (*Agelaius phoeniceus*) (Beletsky and Orians, 1985); white-throated dipper (*Cinclus cinclus*) (Villain et al., 2017); black-capped chickadees (*Poecile atricapillus*) (Otter et al., 2007); European robin (*Erithacus rubecula*) (Tobias and Seddon, 2002); yellow warbler (*Setophaga petechia*) (Moore and Rohwer, 2012)], it seems likely that active negotiation is a more widely spread phenomenon than we realize. Across bird species, there is tremendous potential to investigate the relationship between moment-to-moment behavioral synchrony and life-long patterns of coordination. However, in order to do so, we need to better operationalize behavioral synchrony and coordination during brief social interactions across species and contexts.

INTERPERSONAL COORDINATION IN HUMANS

While behavioral ecology research has largely focused on coordination of activities and movements across hours and days, research from psychology, sociology and anthropology, on humans has had a much stronger focus on moment-to-moment behavioral synchrony during brief social interactions. Such research has focused considerable effort on operationalizing and disentangling concepts associated with the emergent and dynamic nature of behavioral synchrony, or "interpersonal coordination" as it is commonly termed in humans. In human research, the notion that interpersonal coordination is used (intentionally or not) to establish social bonds and connections has existed for over a century, at least since 1912 [(Durkheim, 1912) cited in Rennung and Göritz (2016)]. It has been recognized that the term coordination is difficult to define objectively. The term is used broadly and invokes the notion of harmonious working of multiple components (Bernieri et al., 1994), and carries connotations of cooperation, collaboration, and working-together. The challenge in operationalizing what is altogether obvious, yet surprisingly complex, is reflected in the wide range of specialized terms used to capture aspects of coordination and synchrony. There are over 15 terms used in the literature. In **Table 1**, I define, give examples and key references for, many of these specialized terms. Overall, "coordination" is commonly used to encompass many dynamic and emergent aspects of different features of human social interactions, whereas "synchrony" is a more specialized term that captures the temporal alignment of activities.

From the range of terms presented in **Table 1**, it is evident that there is considerable overlap across the social phenomena being described. However, these terms also capture key differences in dimensions or nuances of interpersonal coordination. The definitions reflect several key important features including, (1) the extent to which movements are temporally aligned and/or simultaneous, (2) the modality or domain of the behavior (and whether other biological or physiological processes are included), and (3) the intentionality underlying the behavioral interaction.

TABLE 1 | Definitions of terms used to describe behavioral synchrony/interpersonal coordination in humans.

Term	Definition	References
Interpersonal coordination	During a social interaction, when the behaviors of individuals are patterned and synchronized; individuals displaying roughly the same behavior at the same time.	Lakin and Chartrand, 2003
	The coordination of postures and mannerisms between social partners.	Vicaria and Dickens, 2016
	Can be divided into behavioral mimicry and interactional synchrony.	Bernieri and Rosenthal, 1991; Rennung and Göritz, 2016
	Spontaneous temporal synchronization of body movements and/or speech between individuals in a social interaction.	Cornejo et al., 2017
	When behaviors in an interaction are non-random, patterned, or synchronized in both timing and form.	Bernieri and Rosenthal, 1991; Cornejo et al., 2017
Synchrony	To perform the same movement at the same time (*Synchronize).*	Tarr et al., 2016
	When two or more events happen at precisely the same time.	McDowall, 1978
	The coordination of movements between individuals in social interactions.	Bernieri et al., 1988
	Coordination of interpersonal behaviors.	Reddish et al., 2020
Interactional synchrony	The flow of movement in the listener is rhythmically coordinated to the flow of speech in the speaker.	Condon and Ogston, 1966; Condon and Ogston, 1967; Kendon, 1970
	When the boundaries of the movement of the listener coincide with the boundaries of the movement of the speaker. The listener and speaker may be making different movements.	Condon and Ogston, 1966; Condon and Ogston, 1967; Kendon, 1970
	The matching of rhythmic behaviors between individuals.	Reddish et al., 2020
	Precise speech-movement and movement-movement coordination between a speaker and listener.	McDowall, 1978
	Movement coordination during social interactions (syn with *interpersonal coordination).*	Bernieri et al., 1994
Intrapersonal synchrony	Synchronization of a person's body movements to their speech rhythm.	Bernieri et al., 1988
Interpersonal synchrony	When the movements of two people overlap in time. However, interpersonal synchrony is not limited to behavioral synchrony, but includes synchrony on neural, physiological, and affective levels.	Rennung and Göritz, 2016
	The matching of rhythmic behaviors between individuals.	Reddish et al., 2020
	The matching of behavior in form and time.	Miles et al., 2010
	When an individual synchronizes their rhythm and movement with another person with whom they are interacting.	Bernieri et al., 1988
	The temporary alignment of periodic behaviors with another person.	Cacioppo et al., 2014
	Instances when two peoples' movements are overlapping in time.	Rennung and Göritz, 2016
Behavioral synchrony	To perform the same action at the same time (*synchronous behavior*).	Dong et al., 2015
	Physically keeping together in time with others.	Baimel et al., 2018
Phase synchrony	*In-Phase Synchrony:* When the actions of each individual are simultaneously at equivalent points of the movement cycle (or a 0° relative phase relationship).	Kelso, 1995; Lumsden et al., 2012; Rennung and Göritz, 2016
	Anti-Phase Synchrony: When actions are simultaneously at opposite points of the cycle (or a 180° relative phase relationship).	Lumsden et al., 2012; Rennung and Göritz, 2016
Behavioral mimicry	When people engage in the same behavior (e.g., mannerisms, postures, motor movements) at the same time.	Chartrand and Lakin, 2013
	Non-conscious behavioral mimicry: The unwitting imitation of another's behaviors.	Lakin and Chartrand, 2003
	Non-conscious behavioral mimicry: Instances in which individuals enact movements previously engaged in by others within the context of a social interaction.	Valdesolo and DeSteno, 2011
Biological rhythms	When one cyclical process is captured by and set to oscillate with another cyclical process.	Bernieri et al., 1988
Motor-sensory interpersonal synchrony (MSIS)	Referring to both the synchronization of motor movements and the synchronization of sensory stimulation.	Rennung and Göritz, 2016
Synchronous multisensory experiences	When individuals have a synchronous sensory experience (e.g., experimental manipulation of touch).	Paladino et al., 2010; Mazzurega et al., 2011; Rennung and Göritz, 2016
Movement synchrony	Non-verbal behavior of one person is highly interrelated, coordinated, attuned, aligned, or synchronized with the non-verbal behavior of their interaction partner.	Bernieri et al., 1994; Tunçgenç and Cohen, 2016; Altmann et al., 2019
Behavioral social synchrony	The coordination of behavior between two individuals (synonym social synchrony).	Kinreich et al., 2017
Emotional contagion	The automatic mimicry and synchronization of another's vocalizations, postures, and movements.	Hatfield et al., 1993
	When a person reads, and spontaneously takes on the emotional and affective state of another.	Chartrand and Lakin, 2013

(Continued)

TABLE 1 | Continued

Term	Definition	References
Behavioral entrainment	The adjustment or moderation of behavior to coordinate/synchronize with another.	Bernieri et al., 1988
Bio-behavioral synchrony	The coupling of individuals' physiology and behavior during moments of social contact.	Feldman et al., 2011; Kinreich et al., 2017
	The coordination of physiological and behavioral processes among affiliated members during social contact.	Feldman, 2015
Brain-to-brain synchrony	Correlations in patterns of brain activity between people.	Hasson, 2016; Kinreich et al., 2017
	Brain to brain coupling: The perceptual system of one brain can be coupled to the motor system of another.	Hasson et al., 2012

The terms presented here come from the fields of psychology, sociology and anthropology and are used to operationalize behavioral synchrony/interactional coordination. This is by no means an exhaustive list of terms used across these fields. The definitions provided in this table are taken with only the smallest changes possible to the wording of the given reference(s), to facilitate readability. From this range of terms, it is evident that there is considerable overlap across the social phenomena being described; however, the differences present across definitions reflect several key important features including: (1) the extent to which movements are temporally aligned and/or simultaneous, (2) the modality or domain of the behavior (and whether other biological or physiological processes are included), and (3) the intentionality underlying the behavioral interaction. It is also noteworthy that there are many instances where research is referenced using consistent terminology of the given manuscript (e.g., interpersonal synchrony), despite the fact that the original reference used a different term (e.g., interpersonal coordination). Additionally, many research articles use terms very generally with little or no definition provided. In particular, synchrony and coordination are often used without definition and/or in the definition of other terms.

However, both terms, synchrony and coordination, can also be used without precise definitions, apparently referring to the same overarching phenomena as well as in the definitions of more specialized terms. For consistency when discussing the range of research on human literature, I will use the term *interpersonal coordination*, [i.e., spontaneous coordination patterns between people during social interaction (Bernieri et al., 1988; Cornejo et al., 2017)] to refer broadly to coordination/synchrony. A key premise in research on human interpersonal coordination is that the social interactions themselves, and not the individuals separately, are typically the unit of analysis (Scheflen, 1982). Importantly, interpersonal coordination is not limited to behaviors alone, but includes physiological and behavioral coordination, and is associated with perception of social success in these moments.

Here, I do not exhaustively summarize the extensive bodies of work on human interpersonal coordination [see recent reviews and meta-analyses (Rennung and Göritz, 2016; Cornejo et al., 2017)]. Rather I aim to (1) provide evidence that humans are easily able to perceive and judge the degree of interpersonal coordination; (2) highlight the unified framework of bio-behavioral synchrony used in these bodies of work and emphasize the reciprocal relationship between physiology and interpersonal coordination; and (3) describe the consequences of interpersonal coordination for social relationships (romantic partnerships and pair bonds). Note that only for aim three will I restrict the discussion to references that have investigated interpersonal coordination between romantic couples, pair bonded individuals. Combined, this discussion is useful for elucidating the shared biological basis of features of synchrony and coordination across humans and non-human animals.

Operationalizing Interpersonal Coordination

A breadth of methodologies have been used to capture and quantify interpersonal coordination in humans (reviewed in Cornejo et al., 2017). These methods range from micro-analysis of video recordings and motion tracking to various physiological measurements. Some of the earliest work was done by coding video recordings frame-by-frame (Condon and Ogston, 1966). Using this technique, researchers highlighted the precise temporal synchrony in movements that occur between speakers in a conversation even if they are not looking at each other (Kendon, 1970). This early work emphasized the role temporal synchrony plays in marking who is participating in a conversation and thus its crucial role in social interaction across contexts (Kendon, 1970).

Over the past several decades there have been many advances in technologies beyond frame-by-frame coding of videos. Now there are several different approaches for automatically scoring temporal synchrony in video recordings. Automatic detection methods have been employed for two decades (Grammer et al., 1999), and continue to be used. These methods have been used across a wide range of social contexts: including to describe the relationship between interpersonal coordination and patient satisfaction in doctor-patient interactions (Ramseyer and Tschacher, 2011), as well as to describe how interpersonal coordination is diminished when two people are arguing (Paxton and Dale, 2013). Movement synchrony has also been captured using motion sensors, such as accelerometers, potentiometers, electrogoniometers, magnetic motion capture systems, and optical motion capture systems. Again, these methods are commonly used today and have been applied to many contexts. Such quantifications of behavioral synchrony or interpersonal coordination have also been linked to psychological factors (e.g., perceived self-other merging, entitativity, liking, and trust) (Paladino et al., 2010; Mazzurega et al., 2011; Rennung and Göritz, 2016; Vicaria and Dickens, 2016). Importantly these behavioral measures are correlated with subjective feelings of synchrony, or connectedness between individuals (Llobera et al., 2016; Preissmann et al., 2016).

Interpersonal coordination, as captured by a range of these above described methods, has been linked to a wide range of physiological measures, including respiration, heart rate, and galvanic skin response to patterns of brain activity. This has been termed bio-behavioral synchrony, which conceptualizes the interrelationship between behavioral and physiological measures of synchrony (Feldman, 2012a). Romantic partners, for example, have been shown to synchronize across these measures: respiration (Helm et al., 2012); heart rate (Levenson and Gottman, 1983); galvanic skin response (Chatel-Goldman et al., 2014); and brain activity (Kinreich et al., 2017). Combined, these varied methods have emphasized how integrated the phenomenon is across behavioral-physiological markers. Furthermore, they highlight the wide range of entry points to study interpersonal coordination across contexts.

Are We in Sync? The Perception of Interpersonal Coordination

Early research on interpersonal coordination cautiously made the assumption that aspects of synchrony were beyond human perception (Condon and Ogston, 1967). Some of the earliest work developed objective criteria for scoring synchrony and experimentally demonstrated that interactional synchrony could be consistently rated by untrained observers (Bernieri et al., 1988). In these early experiments, the only guidance observers were given were brief instructions on how to score three aspects of synchrony:

(1) **Simultaneous movement** – this reflects the quantity or degree of movement that appears to begin or end at the same moment. For example, if a mother begins to turn her head at the precise moment that a child lifts an arm off of a table, it is an instance of simultaneous movement.

(2) **Tempo similarity** – assume that all people have built-in tempos or speeds at which their behavior is set (much like the tempo an orchestra follows at a concert). Rate the degree to which the two people in the clip appear to be "marching to the beat of the same drummer."

(3) **Coordination and smoothness** – assume you are viewing a choreographed dance instead of a social interaction. How smoothly does the interactants' flow or behavior intertwine, or mesh evenly and smoothly?

As given in the rating from page 246 (Bernieri et al., 1988).

Asked to rate social interactions on a scale of 0–9 for each of these three features of synchrony, observers were able to rate social interactions consistently, and expected patterns emerged: for example, mother-infant interactions were rated as being more in sync than those mothers with an infant that was not their own (Bernieri et al., 1988). Untrained observers were also able to rate the degree of interpersonal coordination when only shown the gross features of an interaction (body movements) without seeing the fine details, such as facial expressions and small movements (twitches) (Bernieri et al., 1994). Observer or participant ratings of interpersonal coordination are still commonly used today to investigate the role and impact of interpersonal coordination on a variety of social conditions (Cacioppo et al., 2014; Koehne et al., 2016; Llobera et al., 2016; Preissmann et al., 2016; Koudenburg et al., 2017). Importantly, a recognition of the salient features of interpersonal coordination has led to discoveries that interpersonal coordination can have positive behavioral outcomes even for those not involved in the interaction directly (reviewed in Vicaria and Dickens, 2016).

Behavioral and Physiological Levels of Interpersonal Coordination

The interconnectedness of behavioral and physiological synchrony has been recognized for a long time, and such theories have been well developed, largely coming from early research on mother-infant attachments (Feldman, 2007, 2012a,b, 2015). For mother-offspring relationships, the role of coordination of behavior and physiology on the developing affiliative bond is particularly striking. Through repeated social interactions, parents and offspring become increasingly responsive or sensitized to the physiological and behavioral cues of the other, forming an integrated mother-offspring unit that displays increasing synchronization and forges a selective and enduring attachment (Fleming et al., 1999; Feldman, 2012a). The theory of *bio-behavioral synchrony* has been used to describe these embodied phenomena. During repeated social interactions, individuals' physiological responses such as heart rhythms, endocrine state, and brain activity become correlated and are shaped by the presence of the emerging parent-offspring bonds (Feldman, 2007, 2012a,b, 2015).

Interpersonal Coordination, Prosocial Behavior and Pair Bonding

It has long been known that humans are exquisitely good at synchronizing behaviors during brief social interactions. Adults are capable of behaviorally aligning with any conspecifics including family, romantic partners, friends (familiar conspecifics), and strangers (Feldman, 2012a,b, 2015; Ulmer-Yaniv et al., 2016). This is not surprising since humans are extremely social and maintain many affiliative bonds of varying degrees and types. Interpersonal coordination has been well-described across many types of social dyads including mother-infant, parent-child, doctor-patient, teacher-student, romantic partners, and strangers (Rennung and Göritz, 2016; Cornejo et al., 2017).

Across contexts, interpersonal coordination has been shown to signal interest and positive affect (Bernieri and Rosenthal, 1991); facilitate cooperation (Wiltermuth and Heath, 2009); reflect the relationship of the social partners (Kinreich et al., 2017) and rapport (Lakin and Chartrand, 2003); promote prosocial behavior; and galvanize members of a group to collaborate on tasks (Mu et al., 2017). A recent meta-analysis (Rennung and Göritz, 2016) summarized the results of 60 experimental studies that investigated potential functions of interpersonal coordination. Here the authors distinguish between both motor interpersonal synchrony (when individuals move in sync) and sensory interpersonal synchrony (when individuals receive a sensory stimulation at the same time).

The 60 experimental studies either examined the effect of interpersonal synchrony on prosocial attitudes (i.e., perceived self-other merging, entitativity, unity, closeness, similarity, liking, and trust) and/or on prosocial behavior (i.e., cooperation, conformity, helping behavior, and other-related attention such as social memory). Across these studies, there is strong evidence that interpersonal coordination enhances both prosocial attitudes and behaviors. Importantly, the consequences of interpersonal coordination on prosocial attitudes does not appear to depend on whether the synchronization was intentional; although, intentionality may enhance the effect of synchrony on expressions of prosocial behavior (Rennung and Göritz, 2016). Such a general relationship between synchrony and prosociality may emphasize the role of interpersonal coordination in social bonding very generally. This also raises the question of how the behavioral-physiological process involved in interpersonal coordination between strangers is similar to those between romantic partners.

As with other affiliative relationships in humans, romantic partnerships (pair bonds) are characterized by interpersonal coordination. Similar to the formation and maintenance of parent-offspring relationships, the formation and maintenance of romantic partnerships is also characterized by a concordance in behavioral and physiological synchrony (biobehavioral synchrony) (Schneiderman et al., 2012; Scheele et al., 2013; Ulmer-Yaniv et al., 2016; Kinreich et al., 2017; Sharon-David et al., 2018). Interestingly, some of these lines of evidence for biobehavioral synchrony between romantic partners comes from changes that occur in early parents. For example, in the first year of parenting, first time mothers and fathers develop correlations between circulating endocrine levels (oxytocin) (Feldman et al., 2007), and such hormonal synchrony between mothers and fathers is predictive of family level behavioral synchrony (Gordon et al., 2010). These phenomena parallel some of the patterns described with behavioral and hormonal synchrony in biparental birds, and raise similar questions about our ability to disentangle the coordination of shared parental duties from other aspects of a partnership.

Another useful comparison to understand the effect of romantic partnerships on interpersonal coordination comes from comparisons between romantic partners and strangers. Importantly, small differences in key aspects of micro-social interactions can have profound differences on physiological indicators of synchrony. Kinreich et al. (2017) used hyperscanning EEG to investigate the connections between behavioral and neural synchrony (brain-to-brain coupling). They show that neural synchrony between couples is unique to periods of social interactions (i.e., is not present at rest) and is related to non-verbal cues between couples rather than speech and features of conversations (Kinreich et al., 2017). Couples and strangers did not differ in their overall affect (amount of time spent in positive affect) nor in topics of conversation or amount of time speaking. However, couples spent more time making eye contact, and neural synchrony was higher specifically during these periods of shared gaze. For strangers, neural synchrony was not elevated during periods of shared gaze, however, there was a correlation across dyads in the amount of social gaze and neural synchrony.

Summary

Extensive bodies of work have described the role of interpersonal coordination in human social connections and relationships. Here I have highlighted (1) some of the complexities and nuances that exist in operationalizing, defining and scoring aspects of coordination, (2) the awareness humans have of the extent to which dyads are synchronized, (3) the pervasiveness of synchrony, not only as a behavioral expression, but also as a behavioral-physiological phenomenon at the level of a dyad or group, and finally (4) the effect of pair bonding (and social bonding more broadly) on interpersonal synchrony. For this last point, it is particularly important to note that during very brief social interactions subtle behavioral exchanges can have striking impacts on human connectedness. Again, I want to emphasize that while brain-to-brain coupling in humans is linked to pair bonding, this type of synchrony is not simply an intrinsic response to being bonded, rather it is developed and cultivated over time through repeated social interactions and can also be achieved through other mechanisms such as shared memory or immediate responses to narratives (Hasson, 2016; Chen et al., 2017; Liu et al., 2017; Mu et al., 2017).

A CASE STUDY: ASSESSING BEHAVIORAL SYNCHRONY DURING BRIEF SOCIAL INTERACTIONS IN ZEBRA FINCH DYADS

Above I have discussed the extensive bodies of research from behavioral ecology highlighting the manner in which parental behavior is actively negotiated during brief periods of social interactions, suggesting that moment-to-moment behavioral synchrony may be a key aspect of monogamous partnerships. Furthermore, research from human psychology offers in-depth descriptions of how to conceptualize and operationalize moment-to-moment interactional synchrony and provides robust experimental evidence that behavioral synchrony during brief interactions is key to developing social connections and social bonds. Combined, the above two bodies of work raise the question of how moment-to-moment behavioral synchrony during brief social interactions is related to social bonding in birds and other animals.

Now I turn to some of my recent research, in zebra finches, where I quantify multimodal patterns of behavioral synchrony during brief greets (or reunions). My aim was to describe how pair bonding influenced patterns of behavioral synchrony outside of a breeding context. Greeting (reunion behavior) represents a social situation that is relevant as pair bonds mature (over time, and across breeding stages), as well as across social dyads (with pair bonded mates as well as other flock mates). Ultimately, greeting behavior may provide a relevant social scenario that could be compared across species. The two experiments I discuss below describe how behavioral synchrony (1) is affected by time (over the early stages of pair bonding), and (2) differs across social relationships.

The Ecology and Ethology of Zebra Finches

Zebra finches typically form life-long sexually monogamous pair bonds, but are also socially tolerant and breed and travel colonially (Birkhead et al., 1990; Zann, 1996). They engage in biparental care, and the male and female divide parental duties relatively evenly. Furthermore, zebra finches breed opportunistically and thus make breeding decisions at the level of the pair after integrating multiple social and environmental cues (Perfito et al., 2007; Prior et al., 2013; Prior and Soma, 2015), making the need to coordinate behaviors and reproductive bouts particularly important. Finally, zebra finches have a large repertoire of affiliative behaviors, including dynamic calling behavior, which are used with their monogamous partner as well as other familiar conspecifics (Zann, 1996; Elie et al., 2010, 2011a,b).

Zebra finch pairs do not hold and defend territories, and they remain gregarious. Interestingly, in the absence of an opposite-sex partner they will form equally strong social bonds with same-sex conspecifics, and in the laboratory it appears individuals can also maintain multiple social bonds (Alger et al., 2011; Elie et al., 2011a; Tomaszycki and Zatirka, 2014). Because zebra finches are gregarious, they do not show the increased aggression toward novel opposite-sex individuals that marks the establishment of a pair bond in rodents as described in the introduction. Furthermore, traditional partner preference paradigms may not show selective preference for partners (Prior et al., 2013), although other behavioral assays clearly show that the monogamous bond is selective (Gill et al., 2015; Fernandez et al., 2017).

Assessing Multimodal Behavioral Synchrony in Zebra Finches

Given both the importance of behavioral coordination for monogamous partners during biparental care and the implication of behavioral synchrony broadly in supporting formation and maintenance of social relationships, one might predict that moment-to-moment behavioral synchrony is heavily affected by pair bonding. Furthermore, it would be natural to predict that behavioral synchrony is higher between monogamously bonded individuals than other social dyads. We tested these hypotheses by quantifying multimodal behavioral synchrony during brief social interactions (reunions or greets) (**Figure 1A**) in zebra finch dyads across social conditions (Prior et al., 2019, 2020) (**Figures 1B,C**).

Similar partner separation and reunion paradigms have been used in zebra finches previously (Prior et al., 2014, 2018). We focused on the first 5 min of behavior during interactions or brief reunions following a short (about 3 min) separation or disruption. The finer, moment-to-moment details of these interactions were quantified by recording acoustic data from a tie-clip microphone and movement data from a piezo sensor attached to the perch of a smaller cage along with audio recordings using a single multi-channel Zoom recorder (F8) (**Figure 1A**). Pairs were allowed to freely form in mixed-sex flocks for 72 h (**Figure 1B**). Pair bonding was assessed visually each day: occurrences of selective affiliative behaviors (i.e., clumping, allopreening, and coordinated preening) were scored between individuals during 5 min behavioral observations. Four pairs clearly formed bonds during this time (paired), another four pairs were created from these flocks who were not strongly affiliative (weakly-paired), and two pairs were formed across flocks who had no prior experience with each other (force-paired).

As described throughout this review, there are many ways to quantify the coordination or synchronization of behavior. For these experiments we (1) quantified the similarity in activity levels between individuals within a dyad, (2) calculated sliding correlation coefficients of time-stamped calls (and movements) as a quantification of the temporal synchronization within a dyad, and (3) conducted principal component analyses on activity levels and sliding correlations coefficients (for calls and movements) to describe multimodal behavioral patterns.

With respect to the first hypothesis, we showed calling activity during greeting behavior was highest during initial courtship, and there was a general pattern of decreased activity across the three stages of pair bonding (initial, early, and late pairing) (**Figure 1C**). Despite differences in activity levels, the coordination of activities remained largely constant, however, the two pairs that were force-paired prior to the courtship recording were much less coordinated during the courtship phase (sliding correlation coefficient for calls and movements is shown in **Figure 1D**) (Prior et al., 2020).

With respect to our second hypothesis, we found greeting behavior was affected by social relationship. Familiarity, particularly with females, resulted in more robust and more coordinated greeting behavior. More specifically, monogamous partners, familiar opposite sex dyads, and female familiar same sex dyads were more coordinated in both calling and movement, compared to novel dyads and familiar same sex male dyads (sliding correlation coefficient for calls and movements is shown in **Figure 1E**; Prior et al., 2019). It is also notable that we consistently found females were more active than males, both with respect to call and movement rate (Prior et al., 2019, 2020). These two results are consistent with each other in highlighting that prior social experience rather than pair bonding *per se* modulates moment-to-moment behavioral synchrony.

Summary

These experiments are an early step toward describing multimodal patterns of behavioral synchrony in mundane social interactions across social contexts. The results of the two experiments are consistent in that they suggest that behavioral synchrony is not necessarily enhanced between monogamous partners; but is heavily influenced by prior social experience. Overall, these findings are consistent with the patterns described throughout the review and suggest that behavioral synchrony plays a general role in social relationships rather than being specific to pair bonding. The research described above on behavioral coordination in biparental birds suggests that parental coordination may be more related to sharing parental care rather

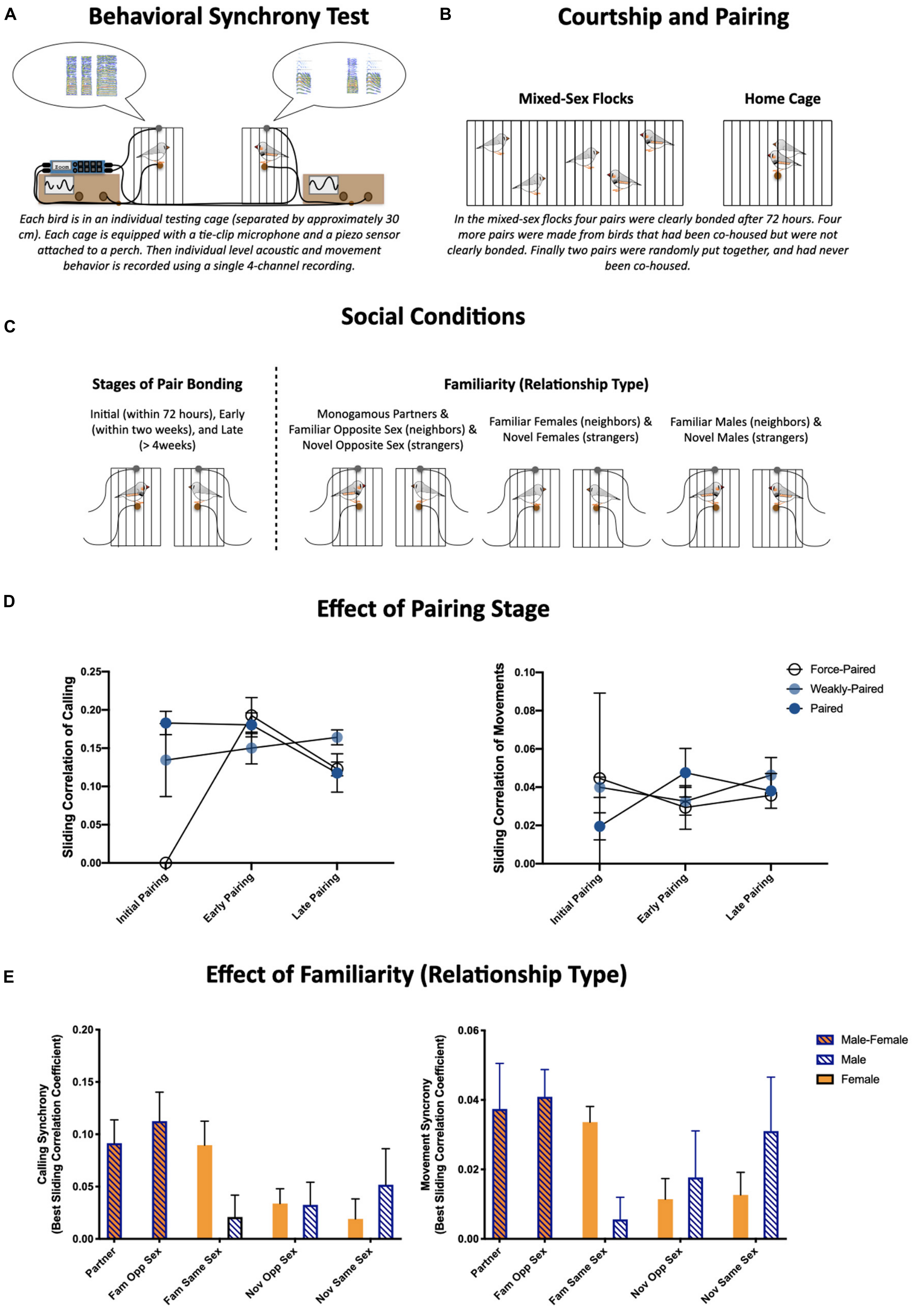

FIGURE 1 | (A) Schematic of the behavioral synchrony paradigm used to quantify behavior during social reunions (greets). The finer, moment-to-moment details of these interactions were quantified from single four-channel recordings of acoustic data from tie-clip microphones and movement data from piezo sensors attached to each perch. **(B)** Illustration of paradigm used to set up pairs. **(C)** We quantified behavioral synchrony during social reunions over the course of pair bonding [initial pairing (4–72 hours), early pairing (within the first two weeks), and late pairing (>4 weeks) (Left)], and across different social relationships (Monogamous partners, familiar same- and opposite-sex dyads as well as novel same- and opposite-sex dyads). **(D)** Effects of pairing stage and prior experience on behavioral synchrony (temporal synchrony based on sliding correlation coefficients) of calls (left) and movements (right) (Prior et al., 2020). **(E)** Effects of social relationship on behavioral synchrony (temporal synchrony based on sliding correlation coefficients) of calls (left) and movements (right) (Prior et al., 2019).

than being an artifact of pair bonding. Additionally, the research described above on interpersonal coordination in humans would be consistent with the notion that higher behavioral synchrony in romantic couples is due to shared experiences rather than an intrinsic consequence of the formation of the partnership.

Combined, these areas of research all point to the importance of shared experience. They suggest that research exploring the shared biological foundations of social alignment may provide a rich basis for comparative studies that investigate the functions of behavioral coordination across timescales, species, and contexts. Such investigations would no doubt require longitudinal studies relating interpersonal coordination (or multimodal behavioral synchrony) over time to other measures of behavioral and physiological synchrony between pairs. Here again, experimental approaches that quantify the effects of a disruption to partner coordination at one level (e.g., parental coordination) on other levels of partner coordination (e.g., hormonal or parental coordination) (Boucaud et al., 2016a,b, 2017) would be important for disentangling different measures and consequences of behavioral synchrony across timescales.

GENERAL DISCUSSION AND FUTURE DIRECTIONS

There are many challenges when it comes to expanding our understanding of pair bonding to incorporate the diversity that exists in pair bonding phenotypes. These challenges are multifaceted, but include: (1) many of the highly marked behavioral variables used are not applicable across contexts and species, (2) the ultimate functions as well as the behavioral and physiological mechanisms underlying pair bonding are confounded with biparental care, and (3) not all affiliative behaviors are equally important. Among a number of possible approaches, one general solution to all three of these challenges is identifying behavioral variables that are relevant across species and contexts. Here I propose using behavioral synchrony as a fundamental aspect of broader sociality, through which we can gain a deeper understanding of the diversity of pair bonding phenotypes across species and contexts.

Comparing patterns of behavioral synchrony in marked interactions of pair-bonded individuals (e.g., monogamous displays, courtship behavior, parental behavior) to behavioral synchrony in general social interactions (such as greetings) could offer a more detailed, nuanced portrait of the dynamic processes of social alignment. The patterns described in this review, including the role of active negotiation during brief social interactions on parental coordination, as well as the impacts of interactional synchrony on brain-to-brain coupling, suggest that behavioral coordination is seen across timescales and physiological levels. Thus, research on behavioral synchrony may prove invaluable for developing an understanding of how pair bonds change over time and are affected by social and environmental conditions. However, before comparing behavioral synchrony across contexts and species, further work needs to be conducted to determine how synchrony is related across behavioral-physiological levels. Importantly, such research needs to put synchrony within the context of pair bonding, and control for potential confounds that come from relating pair coordination to reproductive behavior. Such research lines will contribute to our understanding of whether moment-to-moment behavioral synchrony provides a basis for larger-scale behavioral alignment or vice versa.

When considering the interrelatedness of synchrony across behavioral-physiological levels, it is important to acknowledge that research on the neurobiology of behavioral synchrony is organized very differently than the research identifying neural circuits associated with social bonding. These two bodies of work offer very different perspectives on the neurobiological underpinnings of complex social dynamics. Research on the neurobiology of pair bonding has focused on identifying the key "players": the brain regions, circuits, and neuromodulators that are implicated in the formation of a monogamous bond (Aragona et al., 2006; Alger et al., 2011; O'Connell and Hofmann, 2012; Donaldson and Young, 2016). Neurobiology research on behavioral synchrony, on the other hand, has focused on relating behavioral synchrony to neural synchrony. For example, in the plain-tailed wren (*Pheugopedius euophrys*), neural recordings have demonstrated that the partners' synchronized vocal duet is associated with tight correlation in the partners' neural responses in a cortical brain region associated with vocal-motor integration (Fortune et al., 2011; Coleman and Fortune, 2018). It is particularly remarkable to note that the synchrony of neural firing between mates occurs in response to the entire duet (both female and male components) as a whole, not to each individual component alone (Fortune et al., 2011). It may be that combining these different perspectives on the neurobiology of social dynamics will prove valuable in expanding our understanding of the neurobiology of diversity in pair bond phenotypes. For example, recent research investigating the neurobiology of long-term pair maintenance in prairie voles has benefited from a similarly nuanced approach examining the consequences of pair bonding on brain and behavior (Scribner et al., 2019). These approaches could be combined by studying the consequences of behavioral synchrony or dis-synchrony on neural circuits associated with pair bonding, and reciprocally by identifying the role of pair bonding on neural synchrony between individuals in a dyad.

At the beginning of this review, I suggested that it is easy to assume that behavioral synchrony is positively related to, and perhaps qualitatively unique in, monogamous partnerships. However, throughout this review i have emphasized that behavioral synchrony is critical for all types of social bonds. It is possible that there is something unique about how behavioral synchrony interacts with pair bonding. If there are unique characteristics of behavioral synchrony in pair bonded individuals, it is likely more nuanced than simply the degree of synchrony. For example, it is possible that monogamously bonded pairs more easily regain synchrony following a long-term separation, and/or that the consequences of disruptions to synchrony between partners are greater than disruptions to synchrony between non-bonded individuals. Again, detailed descriptions of brief social interactions and precise quantification and operationalization of behavioral synchrony are needed to determine whether there are in fact unique relationships between behavioral synchrony and pair bonding.

Alternatively, it is also possible that there is nothing specialized about behavioral synchrony during pair bonding. Perhaps what makes pair bonds unique is simply the cumulation of unique shared experiences associated with courtship, biparental care, and long-term coordination of activities and movements. If behavioral synchrony is indeed not specialized in monogamous partnerships, this would argue for a shift in how we conceptualize monogamous partnerships: away from seeing them as extreme and unique social bonds, and toward recognizing that they exist along a continuum of varied social relationships.

Combined, these data suggest that moment-to-moment behavioral synchrony is easily perceptible (Bernieri et al., 1988) and information rich (Elie et al., 2010; Boucaud et al., 2016a, 2017; Villain et al., 2016), and that, even outside of breeding periods, it may promote reproductive success, a traditional metric of pair bond success (Spoon et al., 2006). The extent to which these patterns of synchrony hold within and across contexts and species remains to be tested. However, the existence of such a pattern suggests that regardless of whether behavioral synchrony is somehow specialized to monogamy, behavioral synchrony itself could be a metric of successful pair bonds. Various disruptions to behavioral synchrony could be assessed for their consequences on reproductive success, effects on frequency of extra-pair mating, effects on maintenance of other strong social bonds, and likelihood to divorce.

Altogether, there is overwhelming evidence that "moments matter," and that even brief social interactions can have profound effects on monogamous partnerships. The significance of this conceptual framework is a recognition that pair bonds, as well as of other affiliative bonds, are built upon *repeated* social interactions and experiences and that bonds are co-created in the interactions between individuals, making them intrinsically emergent and dynamic in nature.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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