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All Together Now: Genes, Interpersonal Touch, and Self-Conscious Processes Jointly Guide Cooperative Behavior

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ABSTRACT

Cooperation and trust are critical parts of many relationships. However, such relationships are often studied in siloed ways, leading to incomplete explanations of behavior (e.g., from the point of view of a buyer or a seller, but not necessarily both). This paper makes three contributions to broadening this perspective. First, the authors develop a model incorporating individual differences (genetics), environmental (interpersonal touch), and psychological (empathy and trust) elements to shed light on when and how cooperation is influenced in dyadic relationships. Empathy was predicted to be elicited by the interaction of human touch and the COMT gene to induce, in turn, felt trust and cooperative behaviors. Second, the centipede game is used as a behaviorally relevant context to study how and under what conditions players cooperate while competing with each other. The results of a conditional serial mediation demonstrate that cooperative responses are guided by the interaction of touch and the COMT gene, where empathy and trust are mediators. Actual actions of players are recorded and real behaviors explained. In an additional registered experiment, the mediator, empathy, was manipulated to show that it had a positive effect on trust.

1 | Introduction

Many decision-making contexts feature people interacting with each other for the purpose of meeting individual and collective needs. For example, such interactions can occur in business-to-consumer contexts (e.g., a consumer purchasing a vehicle from a car dealer), business-to-business contexts (e.g., an automaker negotiating with component parts suppliers), or consumer-to-consumer contexts (e.g., via the so-called "sharing economy" whereby consumers can make an item available for other consumers' use, such as on Turo, a peer-to-peer car rental platform). In all of these cases, individuals can choose to pursue distributive (win-lose) or integrative (win-win, or mutually beneficial) consequences. Cooperating to pursue integrative outcomes is often beneficial, as they foster longer-term relationships, reduce the chances of conflict, and lead to better resource allocation (De Dreu et al. 2000). However, working together requires a degree of trust that both parties really are acting to further everyone's interests and not merely their own individual welfare.

A number of research findings suggest that interpersonal touch may encourage parties to pursue mutually supportive outcomes. Restaurant diners who are touched tend to be more generous when allocating tips to their server (e.g., Crusco and Wetzel 1984;

Hornik 1992). Touch from a salesperson (e.g., a handshake) can stimulate trust, and these feelings positively guide product evaluations and purchase intentions (Orth et al. 2013). People who are touched experience greater feelings of security, guiding them to take greater risks and invest money in an allocation game (Levav and Argo 2010). These findings imply that touch can guide people to trust each other and work together in interpersonal decision-making contexts, even when the parties do not have an inherently intimate relationship, such as is typically the case in a sales, services, or negotiation setting.

However, prior work has also shown that touch does not uniformly prompt trust. For example, Martin (2011) found that participants who experienced a brief touch from a passer-by as they were evaluating a product expressed more negative brand evaluations and spent less time in-store. In this context, there are few shared goals and little opportunity for touch to form a social bond. Likewise, characteristics of the individual also seem to influence whether or not touch is facilitative. In their findings described briefly above, Orth et al. (2013) observed a linkage between touch and trust when consumers had a dispositional need for touch (as well as when they were from a culture where touch is relatively rare). Likewise, Webb and Peck (2015) document individual differences in willingness to give and receive interpersonal touch and develop a scale instrument to measure these differences.

Clearly, touch has the potential to positively influence interpersonal decision-making, but the contextual and individual conditions must be right to foster benefits for both or all parties. We build upon these findings and integrate them with a novel context—the centipede game, a multi-move, two-person economic game where players choose between maximizing individual or collective welfare across multiple stages—and a novel biological individual difference—genetics—to shed light on when and why touch fosters trust and eventually cooperative behavior. We further develop an explanatory model to account for cooperation between actors in real exchanges. Our work offers two major contributions.

First, by using the centipede game (Rosenthal 1981), we overcome certain inherent drawbacks of research limited to the study of individual parties (e.g., buyer *or* seller) alone. For example, we investigate actual exchanges rather than traits or decisions of individuals in isolation. We also examine both psychological outcomes and incentive-compatible behavioral outcomes for a more complete picture of both what choices people make and why they make them. Finally, the multi-stage format and consequential nature of the centipede game more closely approximate choice contexts compared to such frequently studied economic games as the prisoner's dilemma, ultimatum, dictator, public goods, and traditional trust games and their many variants.

Second, in addressing why people cooperate or not, we scrutinize a novel set of genetic, environmental, and psychological influences to develop an explanatory model that sheds light on factors that spark cooperation and the psychological route of this influence. We propose that variants of the COMT gene held by participants interact with human touch (where the latter is experimentally manipulated) to contingently activate empathetic concern of participants, which, in turn, stimulates trust enroute to producing real cooperative outcomes. Genetics hold great potential to explain human behavior, but their use in many choice-relevant contexts is still largely unexplored (e.g., in marketing; Daviet et al. 2022). Such potential is particularly acute given the growth of widely available genetic testing via direct-to-consumer services such as AncestryDNA.

We begin this paper by reviewing relevant literature on trust, touch, COMT, and empathy to develop the explanatory model we employ. We then describe results of a study investigating these factors using an incentive-compatible centipede game. Next, we conduct another experiment that manipulates the mediator, empathy, to determine its effect on trust. Finally, we discuss implications of our research and suggest avenues for future investigations.

2 | Literature Review

Over the ages, trust has exhibited different cultural interpretations.

> "Let every eye negotiate for itself and trust no agent."
>
> —William Shakespeare

> "The best way to find out if you can trust somebody is to trust them"
>
> —Ernest Hemingway

> "It is a vice to trust all, and equally a vice to trust none."
>
> —Lucius Annaeus Seneca (circa 60 CE)

Trust is a central concept undergirding social exchanges and can impede or promote the welfare of people or organizations engaged in such exchanges. Yet, as the above quotations suggest, considerable policy disagreements can occur with regard to trust in everyday life, with some advocating that one should never trust anyone, some recommending that one should trust others initially at all times, and still others counseling a middle path as the best advice. Along the latter lines, Lao Tzu (circa 530 BCE) suggested, "He who does not trust enough will not be trusted," implying that trust may depend on interpersonal processes rooted in anticipated reciprocity. But the mechanisms underlining trust have sometimes been relegated to natural tendencies, for example, by the philosopher Ralph Waldo Emerson: "You have first an instinct, then an opinion, then a knowledge ... Trust the instinct to the end, though you can render no reason" (Emerson 2009). Just as there is little consensus about when one should or should not trust others, many questions remain about what factors trigger trust or mistrust in human behavior.

These questions have been studied across a range of disciplines, including economics, psychology, marketing, and genetics. First, a rich and growing body of research in economics points to a myriad of environments that may motivate players in trust games to deviate from actions prescribed by perceptions of rationality under economic theory, but the majority of these studies stop short of offering and testing a theory of the affective and cognitive foundation for how actual trust manifests itself in cooperation. Second, in psychology, many of those foundational building blocks to explain trusting behaviors are present, but relatively little attention has been paid to how they influence trust in most interpersonal choice contexts until recently (Dunning et al. 2014; Simpson 2007). Third, in marketing, while some work has examined the antecedents and consequences of trust in direct customer-salesperson or business-to-business contexts, little progress to date has been made to position our understanding of trust arising from situational and environmental factors. Finally, many elements of feelings, thoughts, and behavior are rooted in genetics and their interaction with the environment (e.g., Caspi et al. 2003; Kitayama et al. 2014), but we are only beginning to understand how biology influences the ways in which people trust and mistrust each other (e.g., Reimann et al. 2017; Zak 2017), especially in business and interpersonal contexts (e.g., Bagozzi and Verbeke 2020; Daviet et al. 2022; Simonson and Sela 2011). We aim to push the frontiers of these extant literatures by investigating and integrating genetic, environmental, and psychological factors that give rise to trust and studying how people make decisions to trust or not trust one another within the context of interactions in the centipede game, where we examine actual behavior as a criterion.

2.1 | What Is Trust and How Can It Be Studied?

Many definitions of trust exist. We start from a behavioral definition proposed by Fehr (2009): "An individual (let's call her the trustor or investor) trusts if she voluntarily places resources at the disposal of another party (the trustee) without any legal commitment from the latter" (p. 238; see also Coleman 1990). At the same time, "… the act of trust is associated with an expectation that the act will pay off in terms of the investor's goals," and results in positive outcomes for investor and trustee: "… if the trustee is trustworthy the investor is better off than if trust were not placed, whereas if the trustee is not trustworthy the investors are worse off than if trust were not placed" (Fehr 2009, 238). As such, in this conceptualization, individuals trust each other by intentionally sacrificing resources to another person with the expectation that one will be better off as a result, at least in the long run. Other scholars have further refined this decision as a willingness to make oneself vulnerable to another person (e.g., Rousseau et al. 1998), and have argued that affect and norm adherence play important roles in the generation of trust (Dunning et al. 2014; Lount 2010). Thus, trust can be conceived as a complex behavioral–psychological–outcome phenomenon.

Trust can be studied fruitfully by use of decision-making games. These games have a long tradition in economics (Berg et al. 1995; Bohnet and Zeckhauser 2004; Camerer 2003; Camerer and Weigelt 1988) and have become incorporated into the psychology literature, as documented by the Cooperation Databank (Spadaro et al. 2020) and a number of individual studies (e.g., Chaudhuri et al. 2003; Dunning et al. 2014; Lount 2010; Piff et al. 2010; Righetti and Finkenauer 2011). While many of these studies employ a single-move trust game, we instead use the multi-move centipede game to examine determinants of cooperation because it features aspects of everyday cooperative and competitive behavior that increase external validity. In everyday life, people often have the opportunity to interact with each other on a repeated basis. In addition, the centipede game has been used relatively infrequently in the investigation of psychological outcomes (e.g., Bornstein et al. 2004; Graf Lambsdorff et al. 2017; Sheldon and Fishbach 2011), to our knowledge. We aim to increase the generalizability of findings on trust by integrating this novel choice context with relevant psychological, genetic, and environmental influences.

In the centipede game (Rosenthal 1981), two players take turns choosing either to take a larger pile of money or to pass the pile to the other participant. When a player chooses to take, that player receives a larger pile of money and his/her partner receives a smaller pile of money. When a player passes, control moves to the other player and the overall payoffs increase. Although each participant has an incentive to take, collective welfare is enhanced if both players wait for a larger payoff. Since the player making the final choice at each opportunity gets paid more from stopping than from passing, standard assumptions of self-interest in economic theory (McKelvey and Palfrey 1995) would suggest that any rational player should use backward induction and choose to take as soon as possible in order to maximize their proportion of total winnings. However, past research has consistently shown instead that players frequently decide to pass control to their opponent, even during later stages of the game (Bornstein et al. 2004; Colman 2003; Colman et al. 2017; Cox and James 2012, 2015; McKelvey and Palfrey 1992, 1995; Rapoport et al. 2003; Zauner 1999).

Even with experience, people often choose to pass control to others. While 70% of professional chess players stopped the game at the first node when matched with other chess players (Palacios-Huerta and Volij 2009), in a directly comparable setting, it has been observed that world class chess players "…exhibit substantial abilities to backward induct in games appropriate for tests of backward induction, but do not choose the backward induction solution in the centipede game" (Levitt et al. 2011, 14). Such behaviors seem to imply that players take into account in their decisions a certain degree of trust that opponents will reciprocate by passing in order to increase collective funds available as behavioral outcomes. However, economic theory does not sufficiently explain the mechanisms behind why people make choices in the ways described above.

We propose that a basis for trust lies in the human wanting system in the brain (e.g., Anselme and Robinson 2016; Berridge and Robinson 2003), and in particular, how polymorphisms of the catechol-O-methyltransferase gene (*COMT* for short) drive trusting behavior. Specifically, we investigate two research questions: How does the *COMT* gene influence passing versus taking behaviors, and when (i.e., under what conditions) does *COMT* influence passing versus taking? To answer the "how" question, we hypothesize that empathy and trust mediate the effects of *COMT* on passing versus taking. To answer the "when" question, we hypothesize that incidental touch by a stranger moderates the effects of *COMT*. Figure 1 summarizes these questions, which we develop below.

2.2 | COMT and the Genetic Basis of Trust

Basic research by neuroscientists identifies the so-called wanting system as a key factor driving reward pursuit, where particular

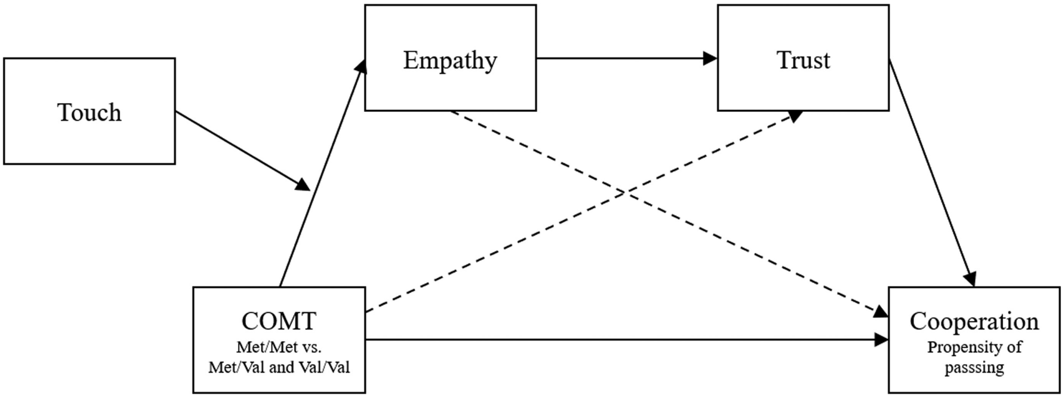

FIGURE 1 | Conceptual model for conditional serial mediation in Study 1.

genes regulate motivation (e.g., Berridge and Kringelbach 2015; Pool et al. 2016). We briefly describe the wanting system and select a promising candidate gene for consideration therein.

The wanting neural network is basically a Pavlovian system of learning where unconditioned stimuli are paired with conditioned stimuli to yield internal expectations and unconscious motivation for rewards (e.g., Schultz 2015). We can think of both winning and monetary outcomes in the centipede game as salient rewards in this sense. As Berridge (Berridge 2009, 378–379) points out, wanting adds "a visceral oomph to mental desires…[and] corresponds best to decision utility…[where it] is needed to color conscious desires, with motivational power, to make them compelling spurs to action."

Neuroscience research reveals that unconscious desires occur in cortical and subcortical brain mechanisms. Desires for particular rewards are governed by the effects of dopamine in the brain. Dopamine is produced by the ventral tegmental area in the brain stem and plays a role in both subcortical (amygdala, nucleus accumbens, ventral pallidum) and cortical (anterior cingulate, insular, orbitofrontal) regions of the brain (Berridge and Kringelbach 2015). Through control of neuroreceptors, dopamine affects cognitive processes and motivation. For example, in the nucleus accumbens, "motivational processes including behavioral activation, exertion of effort, approach behavior, [and] sustained task engagement …" are activated (Salamone and Correa 2012).

The functioning of dopamine in the wanting system is under control of certain genes, such as *COMT*. We conduct what has been called the "candidate gene" approach in the literature which is a theory-based approach focusing on a particular gene (i.e., *COMT*) and can be used with smaller sample sizes than GWAS methods (e.g., Duncan et al. 2014, 249–268). Compared to GWAS, the candidate gene approach is "a different replication strategy … in the attempt to characterize candidate SNP (single nucleotide polymorphism) effects by establishing such effects in a theoretically meaningful nomological net of relevant psychological constructs" (Montag et al. 2020, 169). The GWAS approach searches for significant associations between SNPs and phenotypes, but in our study, we are interested in the interaction between SNPs and our manipulated phenotype, touch. Relevant interaction variables need not by themselves be associated at all in their combinatorial effects on a dependent variable. We focus on findings in the neuroscience literature where candidate neuromechanisms grounding the operation of the wanting system modulate effects on phenotypes.

Drawing upon basic research in experimental genetics, we searched for genes regulating the wanting system. Research in this area is quite new and sparse, but studies show that the *COMT* enzyme "is one of the primary synaptic regulators of DA [dopamine]" (Corral-Frías et al. 2016, 503) and is especially crucial in the wanting system (e.g., Camara et al. 2009; Marco-Pallarés et al. 2010). For example, Lancaster et al. (2012) found, on a reward responsiveness task, that people with the met/met polymorphism of the *COMT* gene showed greater responsiveness to rewards than carriers of the met/val and val/val polymorphisms. The suggestion has been made that the former experience rewards as being more pleasant (and therefore higher in wanting) than the latter (Wichers et al. 2008). This finding has been replicated in a study of probabilistic reward learning (Lancaster et al. 2015).

The functioning of the *COMT* gene is particularly relevant for decision-making game situations where thinking processes are "implicated in decision making and higher cognitive functions [whereby *COMT* achieves] its effects by modulating dopamine-related decision making and reward-guided behavior" (Lancaster et al. 2012, 986). Given the role of the orbitofrontal cortex and the amygdala in the wanting system and for reward seeking, the *COMT* gene plays an important role by supporting higher executive mental processes and working memory (Goldberg et al. 2003), and enhanced positive emotionality and reward seeking (Wacker et al. 2012). In such cases, the met/met alleles increase dopaminergic activity at synapses related to information processing, decision making, and emotion regulation (Lachman et al. 1996), both central processes in decision-making games.

2.3 | Regulating the Effects of COMT in a Trusting Way

Considerable evidence from research on the wanting and reward systems in the brain thus establishes a motivational function for dopamine under control of the *COMT* gene polymorphisms. But how does a proclivity for passing or taking during decision-making games become selected? We propose that aroused motivation can be related to susceptibility toward trusting (passing) versus selfish (taking) inclinations. Based on research by neuroscientists (e.g., Dunbar 2010; Gallace and Spence 2010; Linden 2016) and psychologists (Camps et al. 2013; Hertenstein et al. 2009; Hertenstein, Keltner, et al. 2006; Hertenstein, Verkamp, et al. 2006; Levav and Argo 2010; Thompson and Hampton 2011), we chose human touch as our mechanism for shaping the directionality of dopamine regulation on motivation, because it has been shown to increase the presence of the oxytocin hormone in the brain, which is known to facilitate social bonding (Morhenn et al. 2012), and has been found to lead, through increases in oxytocin, to increased monetary sacrifices in the trust game (Morhenn et al. 2008).

The physiological and psychological mechanisms for the effects of human touch are only beginning to be understood. Linden (2016, 5) speculates that touch is a form of "social glue" engendering human warmth and security, influencing such emotions as sympathy and gratitude, and enhancing cooperation and trust. Some support exists for the hypothesis that touch leads to emotions (Hertenstein et al. 2009; Hertenstein, Keltner, et al. 2006), and, as mentioned above, emotions in the form of feelings of security have been found to mediate the effects of touch on the amount of money invested in an allocation game (Levav and Argo 2010). The interactive effects of *COMT* and touch in the centipede game have not been studied before to the best of our knowledge. Unlike Morhenn et al. (2008) and Morhenn et al. (2012), who investigated the effects of touch in the form of a 15-min Swedish massage where subjects had their shirts raised at the back to their shoulders while lying down, we chose to study the effects of incidental touch so as to examine natural experiences in everyday situations where people engage in competitive and cooperative exchanges (see Method below). Our hypothesis is that brief incidental touch—such as one might encounter in an everyday choice context—will guide dopamine regulation so as to prime participants to be open to social facilitation. As developed below, this occurs through stimulation of natural inclinations to feel empathetic concern for people with whom they interact in the centipede game.

2.4 | Empathy and Trust

Empathy is often construed as an affective trait or state where a person *feels* empathetic concern for the welfare of other people (Batson 2011). Closely related to empathy, and sometimes considered a cognitive component of it (e.g., Davis 1996), is the notion of taking the perspective of another person, which refers to one's ability to *understand* the point of view and even feelings of others. A third possible component of empathy, personal distress, designates a strong aversive emotional reaction to the pain or suffering of another person (e.g., Lamm et al. 2007). In this paper, we focus our attention on empathetic concern because of the unique ability for emotion to motivate action (Bagozzi et al. 1998).

Empathy can be either stimulated by a temporary state or by the activation of enduring personal dispositions (traits) by situational cues. As a familiar example of the latter effect, consider a teacher who is more empathetic when her own child displays disrespectful behavior at home versus when her student displays disrespectful behavior in the classroom. In both cases, the teacher remains the same person with the same underlying traits, but her empathetic response is enhanced or suppressed depending on whether the setting is familial or professional. In turn, because self-judgments are influenced by observations of our own feelings and behaviors (e.g., Bem 1972; Schwarz 2011), the teacher's appraisal of whether or not she has an empathetic personality are likely to be colored, at least in part, by her differing interactions with her child and her student, and influence her ongoing behaviors.

The link between empathy and trust can stem from varied sources: "egoistic concerns (e.g., the desire for reciprocity, a concrete reward, or social approval …), practical concerns (e.g., the desire to prevent waste of goods), other-oriented concerns (e.g., sympathy), or moral values (e.g., the desire to uphold internalized moral values such as those related to the worth or equality of all people or a responsibility for others)" (Eisenberg et al. 2010, 3). Beyond rational explanations for how empathy leads to helping or trust, some research suggests that "feeling empathy for [a] person in need evokes motivation to help [that person] in which these benefits to self are not the ultimate goal of helping; they are unintended consequences" (Batson and Shaw 1991, 114). Indeed, existing research in a variety of domains such as psychology (Joireman et al. 2002), sales/marketing (Aggarwal et al. 2005; Andaleeb 1995; Coulter and Coulter 2003), and medicine (Kim et al. 2004) has linked empathy to feelings of trust.

Finally, trust should positively influence cooperation. A great deal of research has shown that trust facilitates and sustains social relationships; for example, a meta-analysis of over 200 studies demonstrated that trusting expectations of others' behavior yield a strong positive relationship with cooperation, especially when there exist potential interdependent conflicts between one's own outcomes and others' or collective interests, such as in an economic game (Balliet and Van Lange 2013).

Thus, our examination of empathy constitutes specific operationalizations of individual differences of players. Krockow et al. (2016) used the general term "other-regarding preferences" to characterize the broad category of such variables. They found in their analysis of 25 centipede experiments from 1992–2016 that, "other-regarding preferences … provide the most powerful explanation for cooperation" (Krockow et al. 2016, 231). We investigate in Study 1 the interaction of a dispositionally relevant factor (*COMT*) and a situationally relevant factor (touch) on empathetic judgments, trust, and prosocial behaviors.

2.5 | Summary

We propose that the interaction of the *COMT* gene and being touched activates affective empathy (empathetic concern). That is, the effects of motivation and reward seeking, under control of dopamine and regulated by the *COMT* gene, as described above, are channeled by the priming of a social orientation, stemming from human touch, to energize empathy. Specifically, because they are more sensitive to rewards and more effective at regulating emotions, we expect this effect to be most pronounced for *COMT* met/met carriers (as opposed to met/val and val/val carriers). In turn, empathy will guide stated trust and actual cooperative behaviors. The greater the affective empathy, the more trusting participants will be, positively influencing their choice allocation decisions in the game. See Figure 1.

3 | Study 1: COMT and Touch Jointly Influence Cooperation

3.1 | Participants and General Protocol

We recruited participants through subject pools at a large university in the United States. Participants were compensated with partial course credit plus cash winnings from the centipede game. Two-hundred twenty-six participants successfully completed 10 rounds of the centipede game and the follow-up questionnaire described below. Two participants did not supply a usable saliva sample for genotyping and three participants had missing data for components of the mediation model, leaving 221 participants available for analysis.

Participants sat at individual computer cubicles containing a laptop computer and a sheet of paper listing the payoffs for the centipede game. We began the session by administering a set of directions and examples adopted from McKelvey and Palfrey (1992). Participants were asked to follow along on their laptop screen as the experimenter read the directions and examples aloud. As part of the directions, participants were informed that the experiment did not include deception and that their decision outcomes were real. We also instructed participants not to speak with each other during the sessions, and all interactions were accomplished through computer terminals. After the directions and examples were completed, participants completed a brief quiz covering the set-up of the game.

Following the quiz, a female experimenter approached each cubicle to start the centipede game. To ensure that there was no possibility of confounds between touch and experimenters, each experimenter was assigned to separate sections of the experimental lab-space, and the touch/no touch manipulation was induced across alternating cubicles. Each experimental session was conducted by one of six female student research assistants (racial background: 1 Asian descent, 4 Caucasian, and 1 mixed ethnicity). The game was administered using z-Tree software (Fischbacher 2007) and was adapted from a stimulus created by Gerber and Wichardt (2010). We thank these authors for graciously providing us with their original z-Tree stimulus. Participants played 10 games, each with a randomly-selected unique partner identified only by a number. The structure of each game was adapted from McKelvey and Palfrey (1992), except that dollar values were replaced with points, where each point was worth $0.05.

3.2 | Centipede Game

The general structure of the game was as follows. Each participant was randomly assigned to one of two colors (blue or yellow) that determined whether they were to go first or second for all the games in the session. They were then randomly assigned a partner with the alternate color. A pot of points was divided into a small pile and a large pile. The participants who had the first move could choose between one of two options: take the points or pass. If one chose to take the points, then he/she received the large pile, and his/her partner received the small pile. If one chose to pass, then the next move would go to his/her partner, who then would have the same choice to either take the points or pass in the next round. Each time a participant chose to pass, both piles doubled in size. The standard game contained four moves. To preserve fidelity with the design of McKelvey and Palfrey (1992), we also administrated a six-move version of the game and a "high payoff" four-move version where the payoffs from the four-move game were quadrupled, making them equivalent to the last four decisions of the six-move game (see Figure 2). Of the participants assigned to four-move conditions, roughly 28% played the high payoff game, whereas among all participants, roughly 36% played six-move games. The remainder played regular-payoff, four-move games. These differences were controlled for in the analyses.

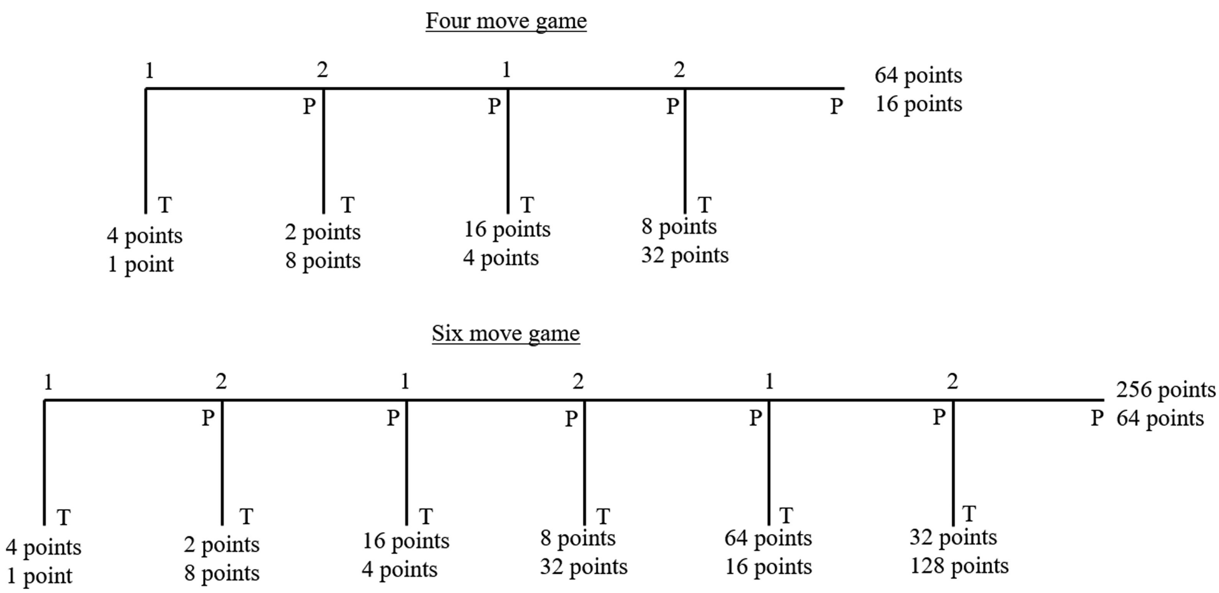

FIGURE 2 | The centipede game formats (P = pass, T = take).

3.3 | Experimental Manipulation

The initiation of the game was accompanied by the implementation of the touch environmental manipulation. In a natural and unobtrusive way, and after approaching the cubicles of participants, the experimenter switched on the active window on the laptop to z-Tree and observed on the screen whether the computer had assigned the participant randomly to the yellow group or the blue group; yellow participants went first in the game, and blue participants went second. The experimenter then verbally reminded the participant, "You will be making the [first/second] move in the game today." In the touch condition, the aforementioned verbal sentence was accompanied by a brief (1 s), light open-palm touch to the back of the left shoulder blade and below the deltoid muscle of the participant, whereas touching was omitted in the no-touch condition.

3.4 | Experimental Procedure and Questionnaire

Participants then played the 10 centipede games with 10 different partners. Participants saw the results of their own previous game(s) but did not receive information about what their partner decided in their previous game(s). After participants completed the games, we administered a questionnaire to measure affective empathy, trust, and socio-demographic variables. Items were selected based on basic research (Baron-Cohen and Wheelwright 2004; e.g., Batchelder et al. 2017; Davis 1983; Lawrence et al. 2004). To measure empathy, we generated 10 items to capture elements of affective empathy, cognitive empathy, and perspective-taking. In this study, we focus on affective empathy, which can also be thought of as empathetic concern, and we selected four items that displayed the best face validity and loadings in a factor analysis (details of the factor analysis can be found in Appendix A and Table A3). The Cronbach alpha reliability of affective empathy items was 0.88. Trust has been measured before by attitudinal or trait items (e.g., Corral-Frías et al. 2016), but we use a state measure of trust to capture how respondents actually felt during the game and in relation to their competitors, which gives a specific game-situated reaction rather than a general disposition. Table 1 presents the items; the full stimulus is available in Appendix B and on ResearchBox (https://researchbox.org/4204). Table 2 presents the means, standard deviations, and correlations of variables for study 1.

After completing the questionnaire, participants donated a saliva sample by use of Norgen Biotek Saliva DNA Collection and Preservation Devices (Model RU49000; Norgen Biotek, Thorold, Ontario, Canada). Finally, participants were paid their earned proceeds (number of total points earned from all rounds multiplied by \$0.05) based on game outcomes and were dismissed. The actual range of earnings was from 36 points (\$1.80) to 768 points (\$38.40).

3.5 | Genetic Analyses

For the genetic analyses, SNP assays were designed in two multiplex reactions, by use of Online Assay Design Suite and Desktop Assay Design Software (Copyright, Sequenom/Agena/Bioscience). Results were analyzed by qualified technicians on the Sequenom Mass ARRAY platform, according to manufacturer's protocols. Briefly, PCR amplification was performed over each design target region, then a single-based extension reaction was performed using a probe oligo adjacent to the polymorphism site. Extension products were purified and analyzed by mass spectrometry to identify the alleles present in each sample. Our analyses focused on *COMT* (rs 4680). We coded *COMT* as met/met = 1 and (met/val and val/val) = −1 for the analyses, which is a common way to study the effects of *COMT* (e.g., Corral-Frías et al. 2016).

We investigated the Hardy–Weinberg equilibrium model (Emigh 1980) to ascertain whether the sample incidence of the three alleles for *COMT* differed from population norms. For our sample, there were 49, 69, and 103 participants, respectively, for met/met, val/val, and met/val genotypes. Computation of the Hardy–Weinberg formula showed a non-significant chi-squared value (x^2 (1) = 0.80, p = 0.37). Thus, the sample did not differ significantly from expected population norms.

TABLE 1 | List of items in model, study 1.

Variable	Items	Scale
Affective empathy (empathetic concern)	(i) I would say that I am a caring person. (ii) Seeing other people in pain bothers me a lot. (iii) When I observe someone suffering I get very upset. (iv) Overall I believe that I am a compassionate person.	Seven-point scale: 1 = does not describe me at all, 4 = describes me moderately well, 7 = describes me very, very well
Trust	Overall, how much trust did you have in the other players' intentions to increase the total money available for both of you to win?	Seven-point scale: 1 = no trust at all, 7 = complete trust
Race	What is your race/ethnicity?	Caucasian = 1 Others = 2
Gender	What is your gender?	Male = 1 Female = 2
Years living in the United States	For how many years have you lived in the United States?	My entire life = 1 Other = 2

TABLE 2 | Means, standard deviations, and correlations for variables, study 1.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1. COMT	—									
2. Touch	0.018	—								
3. Affective empathy	0.006	0.010	—							
4. Trust	0.173*	0.032	0.173*	—						
5. Propensity of passing	0.122	−0.063	0.083	0.390**	—					
6. Centipede game type	0.074	−0.007	−0.039	0.200**	0.413**	—				
7. Participant chose 1st or 2nd	0.004	−0.041	−0.004	0.002	−0.214**	−0.003	—			
8. Race	−0.105	−0.041	0.025	0.035	−0.008	0.064	0.100	—		
9. Gender	−0.016	−0.061	0.255**	−0.080	−0.119	−0.160*	0.079	0.143*	—	
10. Years living in the United States	0.052	−0.055	−0.047	0.147*	−0.036	−0.042	0.030	0.349**	−0.059	—
Mean	−0.557	−0.014	5.598	2.820	0.584	1.900	1.507	1.294	1.440	1.170
Standard deviation	0.833	1.002	1.139	1.633	1.182	0.901	0.5011	0.457	0.498	0.374

3.6 | Dependent Variable Measurement

For cooperation, we created a proportional dependent variable to capture the share of each participant's total cooperative actions, out of all their total opportunities to exhibit such behavior (which was not constant for each participant). That is, the dependent variable was the pass ratio = (total actual passes)/(total opportunities to pass). This proportion ensures that cooperation is properly scaled by each participant's actual number of opportunities to exhibit the behavior. In other words, the pass ratio is each participant's rate of passing as a share of their opportunities to exhibit this behavior across all 10 games. This dependent measure also allows for multiple observations of participants' behavior, which should increase power and reduce measurement error. Given that this is a proportion, it is bounded between zero and one and has some observations "piled" up against the 0 and 1 bounds. In order to analyze this variable as a dependent variable within a linear model, we transformed the pass ratio to be more normally distributed and unbounded by using a logit transformation (Hadden and Jasny 2019; Rubin and Schenker 1987). This transformation essentially reconstitutes one's proportions into "log odds," where for a proportion p, the transformation is log (p/(1-p)). It has been applied to proportional dependent variables in past research under a similar motivation to the one we provide herein (e.g., Hadden and Jasny 2019). However, the above logit transformation does not work for proportions of precisely "0" and "1" i.e., values of 0 and 1 are undefined in log (p/(1-p)). We therefore transform "p" prior to entering it into the aforementioned logit transformation using this formula (Smithson and Verkuilen 2006; Cribari-Neto and Zeileis 2010):

$$New_p = \frac{\left(\frac{Total\ actual\ pases}{Total\ oportunities}\right) * (Total\ opportunities - 1) + 0.5}{Total\ opportunities}$$

where 0.5 is a user specified and can in theory take on any number between 0 and 1. We choose 0.5—which roughly corresponds to a Jeffreys prior—due to its common use in this transformation (Cribari-Neto and Zeileis 2010; Hadden and Jasny 2019). Altogether, this equation accordingly shifts the most extreme (i.e., 0 and 1) proportion values on *p* inwards, while leaving *p*'s less extreme proportion values relatively unchanged. Note however that our key findings and conclusions also hold using the untransformed, proportion-based, dependent variable in our OLS regression models.

3.7 | Results: Indices of Cooperation

In order to facilitate comparisons to research in the literature, in general, and the 25 studies included in the review of the literature from 1992 to 2016 performed by Krockow et al. (2016), in particular, we computed three indices suggested by Krockow et al. (2016), plus two new ones we believe provide further insight. Adherence to the Nash equilibrium was computed for each game as the percentage of games ending in the equilibrium outcome, which occurred for the first terminal node. The second index was the percentage of games which reached the terminal node. Krockow et al. (2016) interpreted this as "the prevalence of altruism," but as we argue below, this index confounds altruism (cooperation) with competition in the sense of maximizing individual gain. We include this second index simply for comparative purposes to findings in Krockow et al. (2016). The third index we compute is the average round completed, which Krockow et al. (2016) consider as an indication of average cooperation levels.

We computed two additional indices. First, we determined the proportion of games ending with passing at the terminal node. Because a participant reaching a terminal node who passes obtains less of an outcome than if they were to take, and at the same time, they provide a greater outcome to the opponent, we interpret this index as a relatively veridical indicator of altruism. Second, we determined the proportion of games ending with taking at the terminal node. Because a participant reaching a terminal node who takes obtains more of an outcome than if they were to pass, and at the same time, they provide less of an outcome to the opponent, we interpret this index as a relatively veridical indicator of a competitive motive based on maximizing self-gain. Table 3 summarizes the indices for each game played and separated for the 4-move and 6-move games, as well as providing averages across all games. It can be seen in panel a that the proportion of participants taking the first opportunity is very low, on average across all games less than 12%. This outcome is comparable to outcomes in similar centipede game experiments in the past (Krockow et al. 2016), suggesting general fidelity with expected outcomes. Panel b of Table 3 shows also the proportion of people reaching the terminal node, which on average was also less than 12% of participants, and which Krockow et al. (2016) interpret as an indicator of altruism. As shown in panel c, however, the actual proportion of participants performing altruistic decisions is quite small: about 2%. By contrast, as displayed in panel d, about 9% of participants opt to take the competitive outcome based on self-gain. Indeed, the competitive to altruistic choice is about 4 to 1. Finally, panel e illustrates the main exit node, which is a measure of average cooperation across games. If we divide these averages by the number of possible rounds (i.e., 4 or 6), we arrive at standardized averages of 0.60 and 0.71 for 4-move and 6-move games. This suggests that players of 4-move games completed on average 60% of possible rounds in these games, and players of 6-move games completed on average 71% of possible rounds in these games. Thus, on average, players completed 65.5% of possible rounds across all games played.

3.8 | Results: Experimental Findings

We used Hayes' PROCESS macro to test the conditional serial mediation shown in Figure 1 (Hayes 2015, 2022; model 83). The following controls were included as covariates. Race and length of time spent in the USA were included to control for cultural differences, as done in the past for analyses of similar games (e.g., Henrich 2000; Roth et al. 1991). Because the majority of participants were "white/Caucasian" (approximately 70%) with only limited representation in each of eight other categories solicited on the questionnaire, we collapsed the eight categories into one, and use white/non-white as our coding. We also controlled for gender based on prior findings showing that women and men sometimes allocate resources differently in decision-making games (e.g., Croson and Buchan 1999; Eckel and Grossman 1996). Finally, to account for aspects of the game environment that were not the focus of our investigation, we controlled for the three game types: (4-move standard payoff, 4-move high payoff, 6-move standard payoff) used by McKelvey and Palfrey (1992) and whether the participant went first or second in the games that he/she played.

The PROCESS macro uses a series of OLS regressions to estimate a sequential indirect path from the independent variable through a series of mediators to the dependent variable, with an interaction included in the first stage of the model (see Figure 1). The PROCESS macro then generates bootstrapped confidence intervals for the index of moderated mediation, which is the critical test of the presence of the hypothesized moderated indirect path. Hayes (Hayes 2015, 3) notes, "A mediation process can be said to be moderated if the proposed moderator variable has a nonzero weight in the function linking the indirect effect of X on Y through M to the moderator … A test as to whether this weight—what I call the *Index of moderated mediation*—is different from zero serves as a formal test of moderated mediation."

Using the PROCESS macro, we ran three regressions: (1) one with empathetic concern (M_1) as a dependent variable, *COMT (X)* and touch (W) as interacting independent variables, and the following controls as covariates: game format (U_1), game order (U_2), race (U_3), gender (U_4), and years in the USA (U_5), (2) a second with trust (M_2) as a dependent variable; *COMT (X)*, empathetic concern (M_1), touch (W), and $X*W$ as independent variables; and the same controls as noted above for the first equation, and (3) a third equation with cooperation or propensity of passing as a dependent variable (Y) and all the aforementioned variables in the first two equations as independent variables. Formally, the equations are:

$$M_1 = i_{M1} + a_{11}X + a_{21}W + a_{31}XW + a_{41}U_1 + a_{51}U_2 + a_{61}\mathrm{U}_3 + a_{71}U_4 + a_{81}U_5 + e_{\mathrm{M1}} \quad (1)$$

$$M_2 = i_{M2} + a_{12}X + a_{22}W + a_{32}XW + dM_1 + a_{42}U_1 + a_{52}U_2 + a_{62}\mathrm{U}_3 + a_{72}U_4 + a_{82}U_5 + e_{\mathrm{M2}} \quad (2)$$

$$Y = i_y + \acute{c}_1X + \acute{c}_2W + \acute{c}_3XW + b_1M_1 + b_2M_2 + b_3U_1 + b_4U_2 + b_5U_3 + b_6U_4 + b_7U_5 + \mathrm{e_y} \quad (3)$$

where i = regression intercept, and a_{ij}, b_i, and $\acute{c}_{\mathrm{i}}$ are estimated regression coefficients.

Table 4 presents the findings for the model testing Figure 1 and Equations 1–3, where affective empathy (empathetic concern) is investigated. *COMT* and touch interacted significantly to influence empathetic concern ($b = 0.26$, $t(212) = 2.93$, $p = 0.004$; column 1). Figure 3 presents a visual summary of the interaction where it can be seen that for the touch condition, carriers of the met/met allele had greater empathetic concern than carriers of the met/val and val/val alleles (effect = 0.28, $t(212) = 2.19$, $p = 0.030$). In the no-touch condition, carriers of the met/met allele had lower empathetic concern than carriers of the met/val and val/val alleles (effect = −0.25, $t(212) = -1.94$, $p = 0.054$). Viewed another way, touch significantly increased empathetic concern for met/met carriers (Effect = 0.43, $t(212) = 2.75$, $p = 0.007$) but did not significantly affect met/val and val/val carriers (Effect = −0.09, $t(212) = -1.09$, $p = 0.277$). Empathetic concern, in turn, significantly influenced trust ($b = 0.30$, $t(213) = 3.17$, $p = 0.002$; see column 2 in Table 4). Finally, trust had a significant effect on cooperation as measured by the propensity of passing ($b = 0.23$, $t(212) = 5.16$, $p < 0.001$; see column 3, Table 4). Further, as the significant index of moderated mediation reveals, the total conditional indirect effect of *COMT* on propensity of passing verifies the proposed mechanisms (index = 0.04; LLCI: 0.0073, ULCI: 0.0807). Thus, not only do empathy and trust mediate the effects of *COMT* on passing versus taking, but incidental touch by a stranger likewise moderates the effects of *COMT* in these respects. Supplementary analyses are available in Appendix A, including mean differences (Table A1) and tests of alternative models (Table A2).

TABLE 3 | Indices of cooperation, study 1.

	Game 1	Game 2	Game 3	Game 4	Game 5	Game 6	Game 7	Game 8	Game 9	Game 10	Average
(a) Proportions of games ending on first move (i.e., in round 1)											
4-move	0.157	0.086	0.071	0.071	0.157	0.143	0.200	0.229	0.271	0.229	0.161
6-move	0.077	0.026	0.051	0.051	0	0	0	0	0	0	0.021
All	0.128	0.064	0.064	0.064	0.101	0.092	0.128	0.147	0.174	0.147	0.111
(b) Proportions of games reaching terminal node (i.e., no matter the choice of move at the terminal node)											
4-move	0.214	0.186	0.200	0.157	0.100	0.071	0.100	0.057	0.057	0.114	0.126
6-move	0.128	0.154	0.128	0.154	0.077	0.103	0.026	0.154	0.077	0.128	0.113
All	0.183	0.174	0.174	0.156	0.092	0.083	0.073	0.092	0.064	0.119	0.121
(c) Proportions of games ending with passing at terminal node											
4-move	0.042	0.042	0.069	0.014	0.028	0.014	0.014	0	0	0.028	0.025
6-move	0.025	0.025	0.025	0.025	0.025	0	0	0	0.025	0.025	0.018
All	0.036	0.036	0.054	0.018	0.027	0.009	0.009	0	0.009	0.027	0.022
(d) Proportions of games ending with taking at terminal node											
4-move	0.167	0.125	0.125	0.125	0.069	0.056	0.069	0.042	0.056	0.083	0.092
6-move	0.100	0.125	0.100	0.125	0.050	0.100	0.025	0.150	0.050	0.100	0.093
All	0.142	0.133	0.115	0.133	0.062	0.071	0.053	0.089	0.053	0.089	0.092
(e) Average round completed (treating games as terminating in round 4 or 6 no matter the final move)											
4-move	2.697	2.648	2.732	2.556	2.352	2.352	2.282	2.077	2.127	2.254	2.408
6-move	4.304	4.519	4.340	4.266	4.203	4.127	4.139	4.190	4.152	4.190	4.247

TABLE 4 | Unstandardized OLS regression coefficients with confidence intervals estimating empathetic concern, trust, and propensity of passing, study 1.

	Empathetic concern (M_1)		Trust (M_2)		Propensity of passing (Y)	
	Coef.	**95% CI**	**Coef.**	**95% CI**	**Coef.**	**95% CI**
COMT (X)	0.01 (0.09)	−0.1667, 0.1893	0.29 (0.13)	0.0378, 0.5394	0.07 (0.08)	−0.0949, 0.2299
Empathetic concern (M_1)			0.30 (0.09)	0.1136, 0.4878	0.05 (0.06)	−0.0727, 0.1722
Trust (M_2)					0.23 (0.04)	0.1398, 0.3126
Touch (W)	0.02 (0.07)	−0.1223, 0.1704				
X x W	0.26 (0.09)	0.0856, 0.4388				
Game format (U_1)	−0.00 (0.08)	−0.1686, 0.1639	0.34 (0.12)	0.1102, 0.5788	0.44 (0.08)	0.2910, 0.5966
Game order (U_2)	−0.08 (0.15)	−0.3770, 0.2118	0.02 (0.21)	−0.3950, 0.4328	−0.49 (0.13)	−0.7584, −0.2289
Race (U_3)	0.02 (0.18)	−0.3365, 0.3709	−0.03 (0.25)	−0.5270, 0.4701	0.04 (0.16)	−0.2823, 0.3557
Gender (U_4)	0.55 (0.16)	0.2412, 0.8529	−0.30 (0.22)	−0.7401, 0.1446	−0.10 (0.14)	−0.3807, 0.1876
United States (U_5)	−0.12 (0.22)	−0.5405, 0.3077	0.67 (0.30)	0.0749, 1.2690	−0.22 (0.20)	−0.6044, 0.1683
Constant	5.05 (0.45)	4.1685, 5.9261	0.14 (0.78)	−1.4025, 1.6746	−0.08 (0.50)	−1.0677, 0.9010
	$R^2 = 0.10$ F(8,212) = 3.06, $p < 0.003$		$R^2 = 0.13$ F(7,213) = 4.52, $p < 0.001$		$R^2 = 0.32$ F(8,212) = 12.67, $p < 0.001$	

Note: Index of moderated mediation = 0.04 [95% *CI*: 0.0073, 0.0807], 10,000 bootstrap samples. $N = 221$. *COMT* and touch mean centered. Standard errors in parentheses

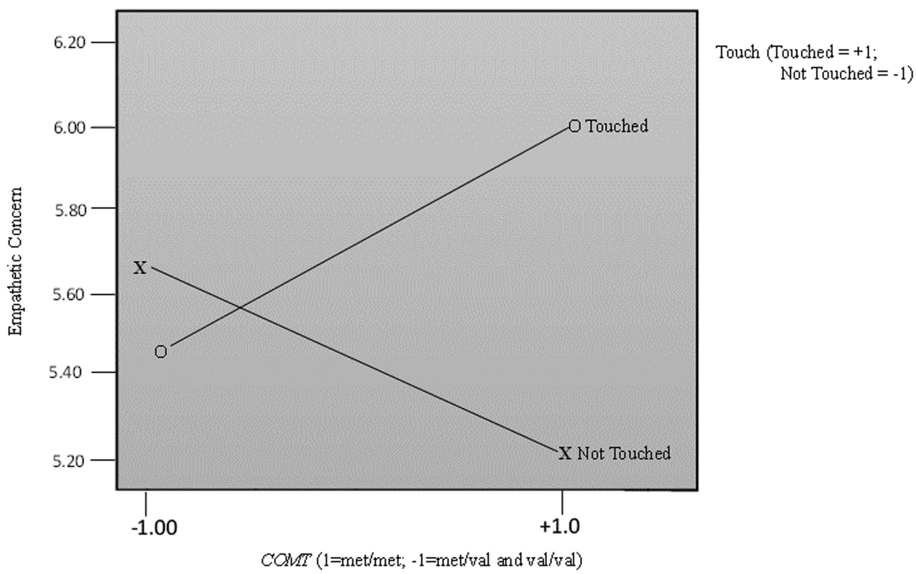

FIGURE 3 | Visual representation of interaction effect of *COMT* and touch on empathetic concern.

3.9 | Discussion

Study 1 reveals a conditional indirect effect demonstrating how a genetic factor (COMT) and an environmental factor (touch) interact to jointly influence the propensity to cooperate via empathetic concern and trust. However, the conditional serial mediation model shown in Figure 1 and tested in study 1 is a complex model. Although the interaction effect between touch and the COMT gene on empathy might be interpreted as causal, the subsequent effects in the analysis are best interpreted as correlational. To provide better support for the model, we conducted a second study where we manipulated empathy and predicted it would have a positive effect on psychological (state) trust. The details of this experiment and the findings are presented below.

4 | Study 2: A Focused Look at Empathy

4.1 | Participants and Procedure

We recruited participants through subject pools at a large university in the United States and administered the study via Qualtrics. The study's protocol was preregistered on aspredicted.org (https://aspredicted.org/5qbr-mb28.pdf) and materials/data are additionally available in Appendix C and on ResearchBox (https://researchbox.org/4204). Participants were compensated with partial course credit. We collected responses from 232 participants, which slightly exceeded our pre-registered target of 225 participants due to variability in participant sign-ups. The study instrument included two attention checks and one data quality question where participants at the end indicated whether or not they attended and responded carefully to the study materials. We excluded 17 participants who failed one or more attention checks or who indicated that they did not complete the study carefully, leaving 215 valid responses based on pre-registered criteria. Subsequently, we also noted that some participants spent very little time on the screen containing the critical manipulation. We excluded six participants who spent less than two standard deviations below the mean manipulation reading time; these participants all read the manipulation for less than 10 s. As reading time was not a pre-registered exclusion criterion, we present the results both with and without these responses. The final analysis set was composed of 209 responses.

Participants were randomly assigned to one of two conditions: an affective empathy condition or a control condition. Following Batson and Ahmad (2001), participants were told that they would receive a note from another person containing details about, "something interesting of a personal nature that they have thought about recently." This note comprised the manipulation. In the affective empathy condition, participants were instructed, "While reading the note, try to imagine how the other person feels about what is described. Try to imagine how it has affected his or her life and how she feels as a result." They then read a note written by a person who planned to attend a farewell party for a friend who is moving across the country, but the plans of the protagonist in the manipulation are thwarted because their basement flooded with terrible smelling sewage, ruining their possessions and necessitating a long wait for a plumber. As a result, the person did not get to say goodbye to their friend and expressed regret, shame, and guilt for letting them down. In contrast, participants in the control condition were instructed, "While reading the note, try to remember that you and the sender will never meet, never see each other, and never know each other's name." While this sender also missed a party due to a sewer backup, the friend was only moving across town; there was no mention of an unpleasant smell or ruined possessions, and the friend was not upset because there would be ample opportunities to see each other later.

Following the experimental manipulation, participants read a description of the centipede game based on the directions for study 1 and were asked to imagine that they were playing such a game with the sender of the note. They then answered a questionnaire about their affective and behavioral reactions.

4.2 | Measures

The questionnaire items are presented in Table 5. Six trust items served as measures of the dependent variable. These were followed by four items measuring trait empathy. Next, we presented participants with a reminder of the empathy manipulation note they previously read and measured their felt state empathy toward the sender of that note. Finally, to mirror study 1, their gender, race (coded for analysis as white/other), and years spent living in the US (coded for analysis as entire life/other) were recorded. Table 6 presents the means, standard deviations, and correlations for variables. The Cronbach alpha reliabilities for the trust, trait empathy, and state empathy scales were 0.84, 0.86, and 0.89, respectively. Note that although trust was asked on a 7-point continuum from completely agree to completely disagree, we reverse-coded these responses so as to have the relationship positively related in the tables.

TABLE 5 | List of items, study 2.

Variables	Items	Scale
Trust	(i) I would trust in the sender's intentions to increase the total money available for both of us to win. (ii) I would trust the sender to make choices that leave us both in a good position. (iii) I would trust that the sender would not make selfish choices. (iv) I am confident that sharing control with the sender would also lead to better outcomes for me. (v) I would be willing to make decisions together with the sender. (vi) I think the potential risk of passing to the sender is justified by the benefits we will both receive.	Seven-point scale: 1 = completely agree, 4 = neither agree nor disagree, 7 = completely disagree. Note: This scale was reverse-coded to facilitate interpretation in the analyses below.
Trait affective empathy	(i) I would say that I am a caring person. (ii) Seeing other people in pain bothers me a lot. (iii) When I observe someone suffering, I get very upset. (iv) Overall, I believe that I am a compassionate person.	Seven-point scale: 1 = does not describe me at all, 4 = describes me moderately well, 7 = describes me very, very well.
State affective empathy	(i) I feel empathy for the sender. (ii) I am bothered by the loss that the sender experienced. (iii) I am upset by the sender's struggles. (iv) I feel compassion for the sender.	Seven-point scale: 1 = does not describe me at all, 4 = describes me moderately well, 7 = describes me very, very well.

TABLE 6 | Means, standard deviations, and correlations for variables, Study 2.

Variable	1	2	3	4	5	6
1. Manipulated empathy	—					
2. Trust	0.14	—				
3. State empathy	0.39	0.21	—			
4. Trait empathy	0.11	0.16	0.54	—		
5. Gender	−0.02	0.02	−0.20	−0.20	—	
6. Race	−0.06	−0.06	0.02	−0.03	0.07	—
Mean	0.01	3.24	4.63	5.66	1.42	1.47
Standard deviation	1.00	1.13	1.27	1.01	0.50	0.50

Note: Coding: manipulated empathy (+1 high; −1 low), trust (recoded for analysis as 1 = completely disagree, 4 = neither agree nor disagree, 7 = completely agree), state empathy and trait empathy (1 = does not describe me at all; 7 = describes me very, very well), gender (1 = female, 2 = male, 3 = other), race (1 = white, 2 = all other).

4.3 | Results: Study 2

Table 7 summarizes the findings for the manipulation of empathy. We conducted two sets of analyses that included and excluded participants who read the empathy scenario very quickly (2SD below the mean; all less than 10s). Panel 1 presents the results for all eligible participants ($N = 215$). Empathy had a marginal effect on trust for both the model with controls ($b = 15$, $p = 0.061$) and without controls ($b = 15$, $p = 0.061$). The key finding can be seen in Panel 2, with excessively fast readers excluded. Empathy had a significant effect on trust for both the model with controls ($b = 0.16$, $p = 0.044$) and without controls ($b = 0.16$, $p = 0.040$). The results in the second panel show that manipulated empathy affects state empathy in both the case with controls ($b = 0.49$, $p < 0.001$) and without controls ($b = 0.49$, $p < 0.001$). This suggests that state empathy underpins the basis for the manipulation and its effects on trust. The third panel reveals that the manipulation does not affect trait empathy in either the condition with control ($b = 0.11$, $p = 0.130$) and without controls ($b = 0.11$, $p = 0.116$). This supports the difference between trait and state empathy.

5 | Discussion

> "We are not students of some subject matter, but students of problems. And problems may cut right across the borders of any subject matter or discipline."
> —Sir Karl R. Popper (1963, 8)

All disciplines have well-defined subject matters, and problems chosen for study tend to be closely situated within the discipline at hand. But seldom is human behavior purely psychological, or economic, or genetic alone. The fullest explanations of behavior often draw upon principles from multiple disciplines because each discipline captures unique causes of behavior not considered by other disciplines. The approach taken in the current paper with respect to analyses and findings is perhaps best interpreted as exploratory rather than confirmatory.

Our approach began with understanding the mechanisms underlying why people choose to cooperate or compete with each other; we expected that touch (as an environmental factor) and genetics (as a biological factor) would interact to influence this tendency. Given the opportunity to act in purely self-interested or cooperative manners, participants in Study 1 were found to often behave cooperatively and trust more in accordance with a range of influences. We found that cooperation is influenced by a process focusing on the genetic control of human motivation within the neuroscience of wanting. That is, we demonstrated that participants who were carriers of the met/met variant of the *COMT* gene, but not carriers of either the met/val or val/val variants, experienced an activation of social facilitation stemming from incidental human touch by a stranger. Specifically, touch activated affective empathy functioning as a disposition, which stimulated trust, functioning as a mental state. Finally, actual cooperation was influenced by trust.

One way to think about the complex processes studied in study 1 is as follows. The human wanting system is propelled by dopamine, which results in the striving for rewards. Reward seeking is proportional to the amount of dopamine in clefts between neurons in such areas of the brain as the orbitofrontal cortex and amygdala. The *COMT* gene is particularly operative as a regulator of this process. We showed both when (i.e., under what conditions) and how *COMT* functions to influence cooperation. Human touch contingently guides the effects of *COMT* because of its stimulation of the need for social affiliation. These positive social orientations are transformed further *en route* to trust of game partners to the extent that participants harbor dispositional empathy. Emotional feelings of concern for others operate in this mediational role. In turn, empathy as a disposition leads to greater trust in participants as a state. Cooperation then follows as an outcome of the biological, social, and psychological processes undergirding the human reward system. In study 2, we augment our understanding of these processes by manipulating state empathy directly, which establishes a causal relationship between empathy and trust, one of the key mediators. This additional insight helps to rule out alternative explanations and sheds light on how these factors interrelate.

Research to date has largely taken a siloed view of how these processes operate. For example, we can ask participants for their self-reported feelings of trust, but unless these are linked

TABLE 7 | Results, study 2.

Effect of manipulated empathy on trust, including readers < 10s ($N = 215$)						
	With controls			**Without controls**		
Variables	***b***	**SE**	***p***	***b***	**SE**	***p***
Constant	3.90	0.40	< 0.001	4.21	0.08	< 0.001
Empathy	0.15	0.08	0.061	0.15	0.08	0.061
Lived in USA	0.32	0.25	0.205			
Race	−0.13	0.16	0.424			
Gender	0.10	0.16	0.524			
Effect of manipulated empathy on trust ($N = 209$)						
	With controls			**Without controls**		
Constant	4.06	0.40	< 0.001	3.76	0.08	< 0.001
Empathy	0.16	0.08	0.044	0.16	0.08	0.040
Lived in USA	0.28	0.24	0.247			
Race	−0.16	0.16	0.331			
Gender	0.06	0.16	0.691			
Effect of manipulated empathy on state empathy (N = 209)						
Constant	5.34	0.40	< 0.001	4.62	0.08	< 0.001
Empathy	0.49	0.08	< 0.001	0.49	0.08	< 0.001
Lived in USA	−0.27	0.25	0.284			
Race	0.18	0.16	0.267			
Gender	−0.49	0.16	0.003			
Effect of manipulated empathy on trait empathy (N = 209)						
Constant	6.23	0.35	< 0.001	5.66	0.07	< 0.001
Empathy	0.11	0.07	0.130	0.11	0.07	0.116
Lived in USA	0.02	0.22	0.922			
Race	−0.03	0.14	0.831			
Gender	−0.39	0.14	0.005			

Note: Trust was measured on a 7-point scale from completely agree to completely disagree and is recoded in these analyses to denote 1 = completely disagree, 4 = neither agree nor disagree, and 7 = completely agree; manipulated empathy versus control is coded +1 vs. −1; Lived in the USA is coded 1 = entire life, 2 = other; Race is coded 1 = white only and 2 = all other categories; Gender is coded 1 = female, 2 = male, 3 = other. All OLS regression coefficients are unstandardized.

to behavioral outcomes, it remains uncertain how closely these responses represent true preferences and actions, since individuals themselves often have scant access to explanations for their judgments and behaviors (Nisbett and Wilson 1977) and people often act in ways that are different than their intentions would suggest (Hulland and Houston 2021). Likewise, we can observe what people do in behavioral situations such as playing the centipede game, but unless we can say how and/or when psychological outcomes like trust emerge, we are left with a lacuna in understanding the etiology of cooperative behavior and the outcomes players receive. What determines here why people trust or not, pass or take, win or lose? Finally, without examining factors that emerge from the environment (such as touch) and individual differences in one's biology (such as genetics), we are left with a relatively incomplete guide to when people are likely to work together and when they are not. Without specifying and testing a theory underlying cooperation that unifies feeling and action, we risk providing explanations that ill-fit observed outcomes. People can become imprisoned by a failure to work together or exploited by unrealistic urges to cooperate with everyone all the time. They can also interact thoughtfully and in accordance with their values, needs, and desires to obtain mutually beneficial outcomes, as found in our study.

We argue that genetics sheds important light on these interactions but at the same time, we note some caveats relating to the complex links between genes and outcomes. First, we acknowledge that genetic influences on psychological outcomes, choices, and behavior are both equifinal and multifinal. Consistent with equifinality, we leave open the possibility that behavior might occur due to multiple genes. Such choices are likely also influenced by a host of other factors, such as other genes, the situation, past experiences, etc. We suggest that our findings be interpreted as a first step at documenting the relationships between the factors under study, and future investigations using other methods are beneficial. In sum, we submit that there is value in documenting the many influences on choices and behavior with these considerations in mind, as together with other findings in the literature, they form a fuller explanatory picture, like individual tiles in a mosaic. Second, in line with multifinality, we acknowledge that although emerging evidence from research shows that genetic variants interact with environment and psychological variables to influence behavior and performance (e.g., Bagozzi and Verbeke 2020), there is a danger in overattributing effects to genes alone, which could lead to prejudice and racial, ethnic, and other biases between individuals. As people learn more about their genetic conditions, there is a danger that they will come to believe that their fate is determined, a priori, and that they have little control over their behavior and outcomes. This could discourage some people during interpersonal interactions such as negotiations and misleadingly cause them to discount the roles that personal motivation and cognitive skills can have in overcoming seemingly fixed effects of gene variants. The functions of genes and personal and social implications of genetic endowment are so uncertain and understudied that caution must be stressed concerning practical and ethical issues underpinning decision making with regard to genetic attributes.

5.1 | Future Research

We attempted to show that part of the etiology of trust is grounded in mechanisms for which people have little or no control. Depending on the variant of the *COMT* gene one is born with, one faces constraints or facilitators that set the stage for subsequent pathways to different behavioral outcomes that are guided by the co-occurrence of a proper environmental catalyst. We studied the effects of incidental touch by a stranger, but other social facilitators deserve investigation, such as the characteristic attachment style (anxious, avoidant, secure; Mikulincer and Shaver 2017) used by people to cope with stress or other genes that might drive motivation, such as oxytocin.

Future research might also examine the evolution or course of trust throughout the centipede game. The perceived trustworthiness of the trustees can theoretically change in response to actions by trustors and vice versa as the game goes on. Certain common communication ploys, such as persuasion or deception, or emotional cues conveyed between players are worthy of future study, but may require altering the centipede game to accommodate more complex interpersonal processes. Social aspects of trust deserve scrutiny, too, such as those found in social network connections (Karlan et al. 2009).

Another direction for future research is to investigate situational or cultural contingencies, as well as individual differences, regulating the course of competition and cooperation in decision-making games (Franke and Park 2006; Lamont and Lundstrom 1977). For example, gender differences have been found in an application of a modified dictator game such that "when altruism is expensive, women are kinder, but when it is cheap, men are more altruistic" (Andreoni and Vesterlund 2001, 293). The economic environment also can affect cooperation, as can how much game participants care about equity (Fehr and Schmidt 1999). Other potential contingent influences on trust might be found in team-based contests, when gamers are members of organizations and differ in social identity with their organizations, and under cultural mind-sets associated with collective, individualistic, and interpersonal orientations.

In many everyday contexts, interpersonal touch is not possible. For example, consumers frequently purchase products online instead of in-store, a real estate agent may interact with buyers via online videoconferencing rather than in-person, and litigants in court trials cannot attain, or even avoid contact with each other, etc. Could touch impact trust in these contexts as well? Recent work has demonstrated that seeing a virtual hand or imagining oneself touching a product (Pino et al. 2020; Webb Luangrath et al. 2022) mimics many of the facilitative benefits of actual touch. Thus, it seems possible that such vicarious touch effects could also extend to an interpersonal context. Future research could examine whether observing touch, such as in an advertisement where the viewer imagines themselves shaking hands with another person, has similar interactive effects with *COMT* as actual touch.

We studied empathy as a disposition in study 1, but it is possible that empathy may be malleable to a certain degree in game contexts and therefore could be investigated as a state as done in study 2. To the extent that participants can elicit sympathy or self-regulate their own empathy, we might expect changes in trust. Emotional changes in players during the course of a game might also be examined. Both positive and negative emotions are likely to arise and affect what happens in a game. Such self-conscious emotions as pride, shame, guilt, embarrassment, and envy (e.g., Tangney and Tracy 2012), and such moral emotions as admiration, awe, elevation, gratitude, righteous anger, contempt, and social disgust (Haidt 2003) might influence trust and actions, and deserve scrutiny. Each emotion mentioned above is engendered by unique conditions and each can shape trust and actions affecting player welfare in different ways.

Finally, economic games, in general, and the centipede game used herein, in particular, provide useful contexts for studying competitive and cooperative behavior. But because they are artificial and may not correspond well with real world behavior, our study may have limitations to external validity. Additional research is needed in the study of competitive and cooperative behavior in more naturalistic conditions than investigated herein.

5.2 | Shortcoming of Interpretating Mediation

A limitation of the present research concerns the interpretation of the role of mediation in tests of hypotheses. Shadish et al. (2002) point out that three criteria are relevant for inferring causality between a hypothesized cause and effect: a cause must precede the effect in time, cause and effect must covary, and alternative explanations for the relationship between cause and effect must be ruled out. Our experiment in study 1 meets these requirements for the dependence of empathy on the interaction between touch and genetic endowment in the COMT gene. Likewise, our experiment in study 2 meets these requirements for the dependence of state trust on state empathy. However, the proposed and observed effects of the mediators do not meet the third criterion for causality and must be interpreted as correlational findings.

Pirlott and MacKinnon (2016) discuss two experimental procedures that could be conducted in addition to our implementation of our moderated mediation model in order to meet the three criteria for causality noted above. Although our study 2 establishes a causal link between empathy and trust, it does not do so while controlling for the hypothesized interaction between touch and the COMT gene variant held by participants. We acknowledge that either of the two procedures proposed by Pirlott and MacKinnon (2016) should be conducted to better interpret the nature of the proposed mediational processes. However, as Pirlott and MacKinnon (2016, 13) caution, a "drawback with this design [i.e., the combination of concurrent double randomization and manipulation-of-mediator designs with measurement-of-mediation design] is that it requires a large sample size – at least enough participants to be randomly assigned to six different conditions, and this potentially undermines its effectiveness in studies with limited funding or participants." Our research is even more sensitive to the drawback pointed out by Pirlott and MacKinnon (2016) who address only mediation models. Because our central hypotheses in Study 1 involve moderation as well as mediation, implementation of the recommendations proposed by Pirlott and MacKinnon (2016) would require sample sizes at least 8–12 times as large as employed in the current research for the conditional measured mediation study, depending on which of the two approaches would be used. The costs of conducting an additional study to unambiguously support the conditional mediational hypotheses are currently considerable.

6 | Conclusion

With the advent of recent advances in neuroscience, genetics, and evolutionary psychology, philosophers of mind and philosophers of science have had to conceive of human behavior in ever more complex ways. An emerging perspective in the behavioral and social sciences in this regard has come to see human behavior from the point of view of *both* object and subject. We are biological objects operating in physical and social environments shaping our behavior. The approach here is a third-person perspective, and our focus on the *COMT* gene and human touch falls well under this point of view. Third-person explanations rely on impersonal causes from outside or inside the mind of people to explain their actions.

But at the same time, consciousness, especially self-consciousness, and intentionality are needed to explain human behavior, because recourse to biology and the environment alone is incomplete and misses the role of interpretation of one's own thoughts, feelings and behavior and those of others with whom we interact (Bagozzi and Lee 2019; Jacob 2023). By intentionality we mean that our awareness of our own mental events and states is toward, of, or about something external to us (Dennett 1987), yet affects how we interpret ourselves in relation to others with whom we are engaged. Human behavior in this sense is intimately a first-person and second-person process: "I trust/mistrust you," "Your welfare is/is not my concern," "I enjoy and value our cooperation and joint goal striving." In our interactions with others, we rely on personal reasons based on our beliefs, feelings, and desires as determinants of our decisions and intentions and as justifications to ourselves and others for what we do or fail to do. Unlike third-person explanations, first- and second-person explanations are built on subjective experiences and involve objective brain processes that ultimately produce subjective representations of meaning in our relationships (Bagozzi and Lee 2019; Smith 2017). We believe that we are responsible or accountable for our actions in relation to others, and self-conscious and moral emotions shape and are shaped by our relationships in this respect. Empathy and trust are but two instances of subjective experience regulating interpersonal behavior in the centipede game.

Real opportunities exist for explaining behavior using genetic and psychological inputs by taking an eclectic approach to research; inter-disciplinary orientations can be an important part of the science of discovery and confirmation in this regard. By combining insights from psychology, economics, and biology, we submit that these findings provide a foundation to better understand trust and cooperation and enhance joint outcomes.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix A:** Study 1 additional analyses. **Table A1:** Mean differences for empathy, trust, and cooperation (propensity of passing) by touch and gene conditions—study 1. **Table A2:** Test of alternative models for Figure 1 and study 1. **Table A3:** Factor loadings for empathy items, study 1. **Appendix B:** Study 1 materials. **Appendix C:** Study 2 materials.