

MULTIDISCIPLINARY PERSPECTIVE ON PROSOCIALITY IN AGING

*Natalie C. Ebner, Phoebe E. Bailey, Marilyn Horta,
Jessica A. Joiner, and Steve W. C. Chang*

Prosociality—A Multi-Faceted, Multi-Level Construct

Humans are genuinely social beings. For the majority of our time, we dwell in social situations or think about self in relation to others. Our social thoughts and actions are directed towards understanding and responding to the thoughts and actions of others. Examples of prosocial interactions in everyday life include experiencing others' emotional distress, volunteering time to help others, offering comfort towards others in physical pain, reciprocating favors, cooperating and sharing goods, or making charitable donations.

Prosociality represents voluntary thought and action intended to benefit others or society as a whole (Brief & Motowidlo, 1986; Dovidio, Piliavin, Schroeder, & Penner, 2006; Eisenberg, Fabes, & Spinrad, 2007). It refers to a variety of biological, motivational, cognitive, and social processes that cover diverse phenomena like empathy, altruism, generativity, reciprocity, cooperation, and trust, and it is measured in various ways, using both scales and experimental paradigms in the laboratory and increasingly also in real-life settings. Thus, prosociality constitutes a multi-faceted construct that comprises different dimensions or subprocesses (e.g., affective versus cognitive empathy) and can be organized on multiple levels (Eisenberg, 2000; Penner, Dovidio, Piliavin, & Schroeder, 2005). The multi-level perspective takes into account the variety of ways in which prosociality has evolved and can be manifested. The "micro level of analysis" refers to determining the neural or evolutionary origins of prosocial thought and action, as well as the etiology of individual differences in these prosocial tendencies. It addresses intriguing questions, such as why help is given to others when there is a cost to one's self, as well as the extent to which evolutionary constructs such as kin selection (Hamilton, 1964), reciprocal altruism (Trivers, 1971), and group selection

(Sober & Wilson, 1999) are involved. These lines of enquiry particularly benefit from a cross-species perspective that targets phylogenetic and ontogenetic levels of development. The “meso level of analysis” examines prosociality in the context of specific helper–recipient dyads, addressing questions such as under what conditions people help each other (Dovidio & Penner, 2001). Finally, the “macro level of analysis” focuses on prosocial actions that occur within the context of groups and large organizations such as reciprocity or volunteering activities in organizational settings (Penner, 2002).

Throughout this chapter, we review research across these different levels of analysis. Adopting a multidisciplinary approach to prosocial thought and action, we bring together social–cognitive, developmental, neuroscience, and evolutionary perspectives. We begin by briefly reflecting on behavioral correlates of complex social-cognitive abilities in non-human primates to further define the construct and to highlight the extent to which these capacities are either uniquely human or shared among species in evolutionary continuum. We then address the question of continuity or discontinuity in prosociality across the adult life span. Finally, we discuss promising directions for future research on aging trajectories in prosocial thought and action and conclude with a brief summary of the current state of knowledge on prosociality in aging and practical implications.

Evolutionary Perspectives on Prosociality and Rudimentary Mechanisms

The presence of prosocial behaviors has long been one of the central interests in comparative psychology, as it has the potential to reveal the evolutionary origin of human sociality. In the past, complex social cognitions and prosocial tendencies were considered uniquely human (Deutsch & Madle, 1975; Mead, 1934). However, accumulating evidence suggests that prosocial behaviors have deep evolutionary origins. That is, non-human primates and rodents display behavioral correlates of complex social cognitions that resemble those of humans (Ben-Ami Bartal, Decety, & Mason, 2011; Warneken & Tomasello, 2006). Integrating levels of analysis, in the following, we briefly discuss some recent advances in studying prosocial behaviors in non-human primates, emphasizing that prosocial behaviors could be traced back in evolution and that non-human primates display rudimentary neural mechanisms underlying prosocial thoughts and actions.

The cognitive demand imposed on coping with complex social structures may have substantially impacted the evolution of the primate brain (Dunbar, 1998). Like humans, many non-human primates live in large social groups with well-defined social structures (Mitani, Call, Kappeler, Palombit, & Silk, 2012). For example, chimpanzees spontaneously form variable patterns of behaviors depending on communities that they belong to, resembling what we call ‘culture’ in humans (Whiten et al., 1999). Furthermore, altruistic helping behaviors analogous to those shown by preverbal children can be found in young

chimpanzees (Warneken & Tomasello, 2006). Such higher-level social behaviors are not limited to the apes but are also found in monkeys (van de Waal, Borgeaud, & Whiten, 2013).

This raises the important question of what is motivating the occurrence of prosocial behaviors and, ultimately, cooperation and social structure, in animals and humans. One possible prerequisite of prosocial behaviors may be a mechanism to process vicarious reinforcement (Bandura, Ross, & Ross, 1963). Cognitive neuroscience research on reward-sensitive neurons in the non-human primate brain (Baez-Mendoza, Harris, & Schultz, 2013; Chang, Gariépy, & Platt, 2013; Haroush & Williams, 2015), combined with neuroimaging results from human studies (Hare, Camerer, Knoepfle, O'Doherty, & Rangel, 2010; Mobbs et al., 2009), suggests that prosocial behaviors in both humans and non-humans might tap into shared neural networks involved in reward-guided behaviors.

In sum, complex social cognitive capacities such as those associated with prosocial tendencies have *analogous* components in humans and non-human primates. In the remainder of the chapter, we adopt an ontogenetic perspective within the adult life span and discuss the extent to which prosociality may change with aging. We focus on evidence for continuity versus change in the two currently most-studied prosocial concepts of empathy and trust in human aging.

Continuity and Change in Prosociality across Adulthood

Human aging is typically associated with decline across a variety of cognitive functions. For example, the cognitive processes of executive control, including inhibitory control, are known to steadily decline with age (Li, Lindenberger, & Sikström, 2001). Recent meta-analytic work on aging and decision making also provides evidence for age-associated decline in learning-based decision making (Mata, Josef, Samanez-Larkin, & Hertwig, 2011) that largely relies on fluid components of cognition (Agarwal, Driscoll, Gabaix, & Laibson, 2009). In contrast, aging is not necessarily characterized by decline in social and affective domains (Scheibe & Carstensen, 2010; Ebner & Fischer, 2014), and although research on age-related change in prosocial thought and action is currently limited, there is emerging evidence that various facets of prosociality remain intact or even increase with age. This may be because prosocial behaviors largely rely on accumulated life experience, and thus crystallized components of cognition, which are less influenced by age.

Research on prosociality in aging is still in its infancy. The majority of current knowledge revolves around the concepts of empathy and trust as fundamental to satisfying social relationships and as critical psychological motivations for prosocial behavior (e.g., see empathy–altruism hypothesis; Batson, 1987; Van Lange, 2015). In the following, we present growing support for age-related decline in cognitive subprocesses of empathy in the presence of stable or even improved affective subprocesses. Furthermore, we discuss recent research suggesting a

possible age-associated decrease in trust sensitivity while self-reported trust increases and trust behavior remains intact.

Enhanced Affective Empathy but Reduced Cognitive Empathy in Aging

Empathy is defined as the capacity to understand others and to experience their feelings in relation to oneself (Decety & Jackson, 2004). It is innate as suggested by evidence that empathic responses can be found in human infants shortly after birth as well as in many non-human species (Preston & de Waal, 2002). Empathy has been shown to facilitate prosocial helping behavior (Eisenberg et al., 1989), which in turn results in better health and well-being, including among older adults (Kahana, Bhatta, Lovegreen, Kahana, & Midlarsky, 2013; Konrath, Fuhrel-Forbis, Lou, & Brown, 2012).

Various definitions of empathy broadly agree on differentiating cognitive and affective subsystems (Decety & Jackson, 2004; Singer, 2006). Cognitive empathy, also labeled empathic accuracy, refers to perspective-taking: that is, the ability to accurately understand another person's point of view, including their thoughts and feelings. It involves higher-order cognitive functions that require self-other differentiation, theory of mind, and autobiographical memory (Preston & de Waal, 2002; Shamay-Tsoory, 2011). Affective empathy, also labeled emotional congruence, refers to the sharing of another person's emotions: that is, the sympathy or vicarious experience of another's feeling states (Batson, O'Quin, Fultz, & Vanderplas, 1983; Davis, 1983). Cognitive and affective empathy have typically been measured either via questionnaires assessing the frequency of empathic feelings or thoughts experienced in daily life (Baron-Cohen & Wheelwright, 2004; Davis, 1983; Mehrabian, 2000) or in the context of experimental paradigms eliciting an empathy-inducing event (e.g., viewing someone suffering from physical distress; Batson et al., 1981).

Empathy may be an important contributor to successful aging, as older compared to young adults tend to afford an increasing importance to social and emotional goals (Carstensen, Isaacowitz, & Charles, 1999). However, evidence linking aging and empathy has been mixed. Aging has been associated with enhancement (Beadle et al., 2012; Sze, Gyurak, Goodkind, & Levenson, 2012), stability (Grühn, Rebucal, Diehl, Lumley, & Labouvie-Vief, 2008), or decline (Bailey, Henry, & Von Hippel, 2008; Noh & Isaacowitz, 2013; Phillips, MacLean, & Allen, 2002; Richter, Dietzel, & Kunzmann, 2011; Sullivan & Ruffman, 2004), depending on experimental conditions including the contextual information available to participants. An inverse U-shaped empathy function in aging has also been observed, in that middle-aged adults reported better empathy than young and older adults (O'Brien, Konrath, Grühn, & Hagen, 2013). Moreover, while cross-sectional self-report studies often suggest age-related decline in empathy (Grühn et al., 2008; Schieman & Van Gundy, 2000), longitudinal evidence supports the idea of stability

across the adult life span (Grühn et al., 2008), suggesting that any decline with age might be a cohort effect, with older cohorts reporting lower levels of empathy than younger cohorts.

The inconsistency in findings regarding age differences in empathy can be resolved somewhat when differentiating cognitive versus affective empathy as well as by looking more closely at the various indices of these empathy subprocesses. In particular, research using standard self-report measures of empathy, such as the Interpersonal Reactivity Index (Davis, 1983), the Empathy Quotient (Baron-Cohen & Wheelwright, 2004), or the Questionnaire Measure of Emotional Empathy (Mehrabian & Epstein, 1972) suggests that older compared to young adults report poorer cognitive empathy (Bailey et al., 2008; Beadle et al., 2012; Phillips et al., 2002). In contrast, some studies have found that older adults may report higher (Sze et al., 2012) or comparable levels of affective empathy (Bailey et al., 2008; Beadle et al., 2012), at least when controlling for intelligence and education (Phillips et al., 2002).

Behavioral measures of cognitive empathy have more consistently documented age-related decline (for a meta-analysis, see Henry, Phillips, Ruffman, & Bailey, 2013), and in some cases, this was linked directly to reduced capacity for inhibitory control (Bailey & Henry, 2008). Innovative recent work has adopted an ecologically valid way to study age differences in cognitive empathy by employing a multi-dimensional approach. This approach goes beyond well-studied constructs such as recognition of complex mental states in static images (e.g., the Eyes test; Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001) by testing the integration of a multitude of inferences from diverse sources of information such as facial and bodily expressions, prosody, communication content, and situational contexts. Notably, there is a significant amelioration of age deficits in empathic accuracy when integration of manifold and complex pieces of information in everyday interactions is possible (Blanke, Rieurs, & Riediger, 2015; Rieurs, Blanke, & Riediger, 2013). For example, Rieurs and colleagues adopted a dyadic approach to assess empathic accuracy in young and older couples' daily lives. Although young adults' empathic accuracy was higher than older adults when their partners were visibly present, the age groups did not differ in empathic accuracy during their partner's absence—that is, when their judgments relied exclusively on knowledge of their partner. Empathic accuracy therefore seems to rely not only on the adequate perception of sensory cues, such as emotional expressions, but also on acquired knowledge, a capacity that may benefit from accumulated life experience associated with aging (Ickes, 1993; Sze et al., 2012).

Mimicry response represents an early stage in the process of experiencing affective empathy or may be a facilitator of affective empathy (Decety & Jackson, 2004) and has been shown to increase prosocial behavior (van Baaren, Holland, Kawakami, & van Knippenberg, 2004). Young and older adults show equivalent levels of facial expression mimicry regardless of whether the images of the faces are static or dynamic, or are presented subconsciously or consciously (Bailey, Henry, &

Nangle, 2009; Bailey & Henry, 2009). Intriguingly, there is also evidence for age-related enhancement in the mimicry of smiles (Slessor et al., 2014) and expressions of disgust (Hühnel, Fölster, Werheid, & Hess, 2014). Thus, in some situations, older adults are more likely than young adults to mimic facial expressions with congruent expressions, and this is further evidence for enhanced empathy in advanced age.

Context Dependency of Age-Related Changes in Empathy

Context dependency has been determined as a critical factor that influences age differences in empathy, particularly when measured in the form of empathic concern (O'Brien et al., 2013). Wieck and Kunzmann (2015) assessed age-related differences among women when responding to people recounting autobiographical memories that systematically varied in age relevance (topic relevant to young versus older adults) and emotional quality (anger, sadness, happiness). Older, compared to young, women were less accurate in perceiving others' emotions presented in short film clips. Remarkably, this age deficit was no longer present if the portrayed emotional experience was of high relevance to older adults, supporting a critical role of context in shaping empathy across the life span. Similarly, Richter and Kunzmann (2011) showed that, when hearing others talk about emotionally engaging topics, emotional congruence was stable with age, and even increased when the topic of conversation was of high relevance to older adults (i.e., a 'social loss' as opposed to 'life transition' theme). By contrast, an age-related increase in self-reported and expressed (i.e., compassionate listening behavior) sympathy was not moderated by age relevance, suggesting that sympathy might be more experience-based and automatic compared to emotional congruence (i.e., less sensitive to age-related decline).

Empathy in itself has been revealed as a social context that plays an important role in older adults' prosocial behavior. Sze et al. (2012) found a linear age-related increase in personal distress in response to a distressing film. However, they also identified a linear increase in affective empathy with age, as indexed by self-reported empathic concern and physiological responding (cardiac interbeat interval, systolic blood pressure, and skin conductance), as well as in subsequent prosocial behavior. Furthermore, empathic concern, physiological activity, and experienced distress were all associated with an increase in charitable donations, but only empathic concern mediated the age-related increase in this prosocial behavior. Similarly, a study by Beadle, Sheehan, Dahlben, and Gutchess (2013) induced empathy with two notes; one from someone describing their experience with cancer (empathy induction), and another from someone describing their daily errands (neutral control). In two subsequent dictator games, in which participants were endowed with a sum of money that they could keep or share, older adults were more likely than young adults to propose generous splits of money

when empathy had been induced. While there were no age-related differences in self-reported affective empathy, this index was more strongly associated with empathy-induced prosociality among older relative to young adults. Although empathy induction is not always required to observe an age-related increase in the extent of prosocial behavior in the dictator game (Roalf, Mitchell, Harbaugh, & Janowsky, 2012), the work by Beadle and Sze and their colleagues demonstrates the importance of social context in eliciting prosocial behavior in older adults.

Cultural influences may also play a role in the effect of empathy on older adults' prosocial behavior. While Beadle and colleagues (2013) tested a Western sample, Rieger and Mata (2013) induced empathy by informing participants from rural communes in Morocco that money they would be donating in a dictator game would go to a poor family. However, they observed no effects of age on prosocial behavior in their sample.

Neural Basis of Age-Related Changes in Empathy

Determination of age differences in the neural mechanisms purporting empathy can further advance our understanding of prosociality and aging. Overlapping but non-identical neural bases including a variety of neuromodulators underlie the distinction between the cognitive and affective empathic subprocesses (Fan, Duncan, de Greck, & Northoff, 2011; Shamay-Tsoory, 2011). There is emerging evidence that the dopaminergic system may be primarily associated with cognitive empathy (Lackner, Bowman, & Sabbagh, 2010) and the oxytocinergic system may primarily modulate affective empathy (Hurlemann et al., 2010). While the left anterior insula has been found to be active in both cognitive and affective empathy (Fan et al., 2011), areas such as the dorsolateral and ventromedial prefrontal cortex, temporoparietal junction, and the medial temporal lobes have been identified as key regions associated with the cognitive component of empathy (Shamay-Tsoory, 2011). Activation in these brain areas also facilitates cognitive empathy when the object of empathy must be held in mind and alternative interpretations must be considered, as well as when cost/benefit analyses are required to decide when to engage the empathy system and act prosocially.

Currently, research on the neural circuits underlying empathy in older adults is remarkably scarce. Some evidence suggests that partially distinct neural substrates underlie cognitive and affective empathy in older adults. In particular, older adults with higher levels of affective empathy showed more deactivation in the amygdala and insula during a working memory task, whereas those older adults with higher cognitive empathy showed greater insula activation during a response inhibition task (Moore et al., 2014). In addition, there may be age differences in the neural networks involved in processing empathy-inducing stimuli (Chen, Chen, Decety, & Cheng, 2014). Young, middle-age, and older participants viewed video clips of body parts in either a neutral position or being injured accidentally or intentionally. Age-related decline in the empathic response to another's pain

correlated with reduced activity in the anterior insula and anterior mid-cingulate cortices. However, preservation of the response to agency in aging (older adults rated intentional pain as more unpleasant than accidental pain) was associated with activation in the medial prefrontal cortex and posterior superior temporal sulcus. This suggests reduced affective sharing yet preserved cognitive empathic understanding in aging (in contrast to some previous work; e.g., Sze et al., 2012). Furthermore, there was a double dissociation in that for older adults, unpleasantness ratings were positively correlated with increased activation in the anterior mid-cingulate cortex, but not in the posterior superior temporal sulcus, while for young adults, this pattern of brain activation was reversed. This finding suggests that there may be a dramatic shift in how the brain processes cognitive and affective empathy with age.

Beyond Empathy: Increase in Self-Reported Trust and Reduced Trust-Sensitivity in Aging

Trust constitutes another important promoter of prosocial action (Van Lange, 2015), and is currently a largely understudied aspect of social relationships in older adults. Recent multi-country surveys identified age-related increase in self-reported interpersonal trust in both cross-sectional (Li & Fung, 2013) and longitudinal (Poulin & Haase, 2015) data. This increase in trust was associated with greater well-being, particularly among older adults who appear motivated to enhance emotional connectedness with others. Also, there is evidence that older compared to young adults are more likely to follow the eye gaze of trustworthy-looking than untrustworthy-looking faces (Petrican et al., 2013) and are less likely to take into account untrustworthy reputations when investing money (Bailey et al., 2015a), possibly reflecting increased attention to cues of trustworthiness and/or decreased sensitivity to cues of untrustworthiness. This age-related difference in the processing of trustworthiness is in line with age-related positivity, and more specifically, evidence for reduced attention to negative compared to positive information in aging (Carstensen, 2006; Reed, Chan, & Mikels, 2014).

Contributing to this attentional change may be the difficulty that older adults have in "reading" the emotions of others, as suggested by age-related difficulty recognizing threat in faces (Ruffman, Sullivan, & Edge, 2006), as well as the mediation of older adults' lie detection difficulties by poor facial emotion recognition (Ruffman, Murray, Halberstadt, & Vater, 2012; Stanley & Blanchard-Fields, 2008). Older adults are also less able to recognize facial cues of untrustworthiness and show a decrease in anterior insula activity (i.e., "gut feelings") in response to these facial cues (Castle et al., 2012). This may render older adults less sensitive to signs of deception and may thus put them at increased risk for exploitation.

Of note, however, a recent review by Ross, Grossmann, and Schryer (2014) concludes that there is no compelling evidence that older adults are disproportionately victimized by consumer fraud. Rather, in everyday life, possible protective

factors associated with old age, including increased experience and changes in goals, lifestyle, income, as well as purchasing and risk behaviors, may counteract any insensitivity to trustworthiness. However, Ross et al. (2014) acknowledge that consumer fraud involves putting trust in strangers, and future research needs to assess the extent to which older adults' trust may be differentially exploited by strangers compared to close friends and family or people who establish a relationship with them over repeated interactions. This is particularly important in light of substantial evidence that older adults are susceptible to elder abuse and thus financial exploitation by those with whom they are in an existing or cultivated relationship of trust. For example, in representative national samples in America and Australia, prevalence of financial abuse is estimated to occur in around 5% of the older adult population, but is also described as both chronically under-reported and the fastest growing form of abuse (Lowndes, Darzins, Wainer, Owada, & Mihajlicic, 2009; Laumann, Leitsch, & Waite, 2008). These data are indicative of older adults being at high risk of financial mistreatment from people who are actually familiar to them (Laumann et al., 2008).

Insights from Economic Games on Trust and Aging

While there is evidence for an age-related increase in self-reported trust as well as age-related decrease in trust-sensitivity, behavioral studies administering anonymous one-shot trust games largely agree that aging is not associated with ever increasing trust and prosocial behavior. Rather these studies propose no influence of age on the propensity to trust (Bailey et al., 2015a; Holm & Nystedt, 2005; Rieger & Mata, 2013; Sutter & Kocher, 2007). While Sutter and Kocher found that trust increased almost linearly from early childhood to around the age of 30 or 40 years, it remained constant in older age groups (also see Fehr & Fischbacher, 2003; Fehr & List, 2004). Economic trust games use game theory to model trust and cooperation (Berg, Dickhaut, & McCabe, 1995). In the trust game, player 1 decides how much of an endowment to give to player 2, while knowing that this investment will be multiplied by the researchers. Player 2 can then decide how much of the increased investment to return to player 1. Thus, player 1's initial investment with player 2, in the hope of receiving the same amount or more in return, is an index of trust. There is evidence that when information is explicitly provided about the untrustworthiness of player 2, older adults invest more than young adults in the trust game (Bailey et al., 2015a). This age-related increase in trust could be attributed to age-related positivity and reduced attention to negative information, as discussed before. However, the difference between young and older adults may also reflect an age-related decline in punitive action as older adults attempt to maximize their emotional well-being by worrying less about losing small amounts of money in the context of the laboratory game.

Trust and trustworthiness may involve both altruism and the expectation of reciprocity from others in uncertain or risky situations. However, trustworthiness

might rely the most on altruism. Although young and older adults generally do not differ in trust game investments, older adults are more likely than young adults to demonstrate trustworthiness (Bailey et al., 2015b). Notably, as shown in Figure 13.1, this is contextually dependent since there is an age-related increase in the proportion of investments returned to investors (i.e., trustworthiness) only when older adults are potentially interacting with their own age group (i.e., age-based in-group). This is consistent with Sutter and Kocher's (2007) finding that older adults are more trustworthy than young adults during same-age trust game interactions. Other studies found no age-related difference in trustworthiness in trust games (Holm & Nystedt, 2005; Rieger & Mata, 2013), but these studies did not provide any explicit information about the recipients of the trustworthy behavior (e.g., own-age versus other-age). In the study by Bailey et al. (2015a), older adults' increased trustworthiness was only evident when participants interacted anonymously, although they received general information about the age group of their interaction partner. No effect of age on trustworthiness was found in face-to-face interactions. Interestingly, this effect seems to be driven by the behavior of the young adults rather than the older adults. The data suggest that, in contrast to young adults, older adults may have been relatively unconcerned with adjusting their trustworthiness in light of reputational implications, or may have been satisfied with any potential reputational implications in both the anonymous and face-to-face conditions. Also of note, older adults' trustworthiness towards

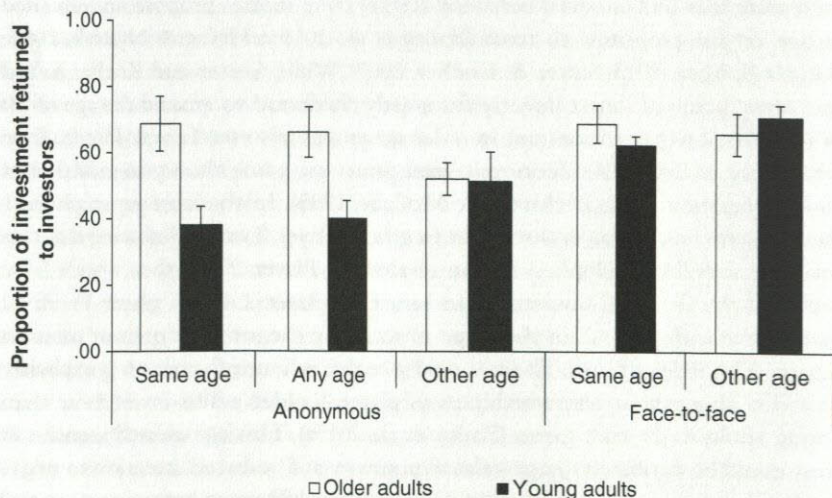


FIGURE 13.1 Proportion of investment returned to investors by trustees in a trust game (i.e., trustee trustworthiness) is larger for older relative to young adults when investors are from a group that may contain individuals of the same age. This age effect is evident in anonymous but not in face-to-face trust game scenarios.

Note: Bailey et al. (2015b).

members of their own age group was associated with subjective feelings of financial well-being, but not with reported income. Indeed, age per se may not be the major driving force behind age differences in trust-related prosocial behaviors because factors such as education and wealth also differ starkly between these groups (Johnson & Mislin, 2011). Future social economic studies that assess age differences in social cognition and prosocial behavior should therefore carefully control for these variables.

Other social economic games also hold the potential to assess prosocial behavior in the context of aging. In particular, Rieger and Mata (2013) found a concave relation between age and the likelihood of contributing to the public good in a public goods game. This suggests that feelings of obligation toward the group may increase between young and middle-aged cohorts but then decrease for older cohorts. In an ultimatum game, participants must decide whether to accept or reject a proposed division of money. Critically, accepted offers mean that both players are paid, while rejected offers mean that no one is paid. Unfair divisions of money are often rejected, and acceptance of such an offer may, in some cases, be considered prosocial in that it delivers a benefit to the other person. Bailey, Ruffman, and Rendell (2013) found that, relative to young, older adults accept more unfair monetary offers from young adults. Other studies found either no age-related differences in the tendency to reject an unfair offer (Nguyen et al., 2011), an age-related increase (Roalf et al., 2012), or variable outcomes depending on the extent of the unfairness (Harlé & Sanfey, 2012). Interestingly, Beadle et al. (2012) showed that older adults are less prosocial than young and reject more unfair offers when they are high rather than low in self-reported cognitive empathy.

Taken together, economic games comparing older and young adults have revealed that behavior that may at first appear economically irrational can be explained as socially and emotionally rational in the context of strengthening social ties and feelings of emotional well-being in older adulthood. However, further research is needed to delineate the various contextual influences on older adults' behavior in these games.

Promising Avenues for Future Research in Aging and Prosociality

In the following, summarized in Box 1, we discuss selected topics, across the various representational levels (Penner et al., 2005), that, to our belief, have a great potential to advance understanding of aging effects on prosociality but have not yet been sufficiently addressed in the literature.

As supported by evidence reported throughout this chapter, it will be informative to systematically differentiate prosocial tendencies towards (e.g., age-based) in-group members from those towards out-group members as well as towards close others over strangers. This research has the potential to clarify the impact of social relationships on prosociality in aging. As noted, there is evidence that older

compared to young adults with high cognitive empathy are less likely to engage in prosocial behavior with strangers (Beadle et al., 2012). It is possible that this pattern of findings would differ if prosociality was targeted toward close others who represent more emotionally meaningful social connections. Work by Carstensen (2006) proposes that motivational orientation changes across the adult life span in that close emotional relationships, as compared to informal acquaintances, increase in relevance with age. Therefore, prosocial thought and action in response to close others compared to strangers may vary across age. In this context, it will also be interesting to integrate research on age-related increases in generative, particularly intergenerational, commitment (McAdams, de St. Aubin, & Logan, 1993) as an important contributor to successful aging (Villar, 2012).

We also propose that there is a need to consider the influence of culture on prosocial tendencies across different phases of the life span. The majority of empirical work on prosociality and aging is based on Western populations. Intriguing recent work, however, suggests that cultural contexts may influence the relationship between age and prosociality (Rieger & Mata, 2013), thus questioning the universality of, or at least the cultural independence, of prosocial thought and action and emphasizing the role of socialization. For example, there is evidence that North American and Asian populations are typically more prosocial than African populations, possibly related to cross-cultural differences in the social structures and prevalent incentives for prosocial behavior (Henrich et al., 2005; Johnson & Mislin, 2011). Relatedly, a greater research focus on everyday life prosociality that allows for integration of naturalistic and comprehensive environmental information is warranted to increase the ecological validity of the findings (Blanke et al., 2015).

Further potential contributing factors to age-related differences in prosociality that future research must systematically address are interindividual variations in personality traits (e.g., openness, risk-preference) (see Mata et al., 2011) as well as cohort effects that may be tested in longitudinal examinations spanning the entire adult life span to allow for determination of onset and patterns of change. Also, future research needs to aim for increased comparability across studies, reducing the impact of task variations. Although some studies find consistent effects across several measures of economic behavior (Anderson & Mellor, 2008; Dohmen et al., 2011), there is a debate about the ability of economic measures to capture underlying preferences stemming from the lack of empirical association between different games (Berg, Dickhaut, & McCabe, 2005) and variability of results as a function of procedural variation within games (Bardsley, 2007; Dana, Weber, & Kuang, 2006).

We also believe that a better understanding of the neurochemical environment of the brain associated with aging would propel this field forward. Research suggests that mammalian social behaviors originate from reproductive functions. These behaviors were repurposed over the course of evolution for the development of more complex social behaviors (Chang, Brent et al., 2013;

Pedersen, Chang, & Williams, 2014). Accumulating evidence suggests that the neuropeptide oxytocin, an evolutionally-conserved neuromodulatory hormone (Donaldson & Young, 2008), may be a biochemical mechanism that controls differential expression of social behaviors across the adult life span. Current examination of behavioral correlates and brain mechanisms associated with age-related change in level and function of oxytocin in aging is extremely sparse (Ebner,

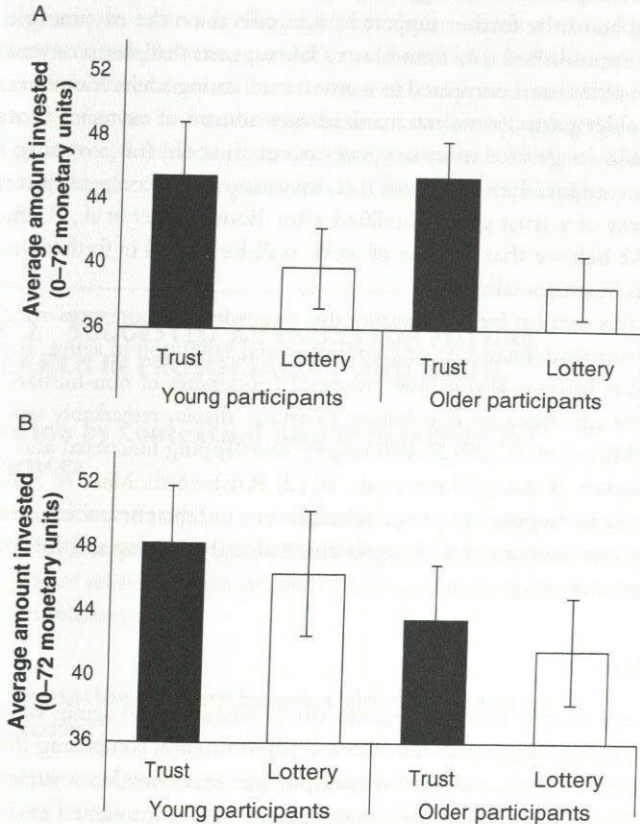


FIGURE 13.2 In a trust game, intranasal administration of oxytocin modulates monetary investment in social (i.e., investing into fellow players) compared to non-social (i.e., investing into a computer lottery) trials. **A.** Oxytocin condition: In the group of young and older participants who administered intranasal oxytocin spray prior to task engagement, monetary investment was greater in social compared to non-social trials; this effect was particularly pronounced in older participants. **B.** Placebo condition: This effect did not hold in the group of young and older participants who administered the intranasal placebo spray prior to task engagement. Error bars represent standard errors.

Note: Ebner et al. (unpublished data).

Kamin, Diaz, Cohen, & MacDonald, 2015; Ebner, Maura, MacDonald, Westberg, & Fischer, 2013; Huffmeijer, van Ijzendoorn, & Bakermans-Kranenburg, 2013, for reviews). Intriguingly, preclinical work suggests that aging may be associated with a reduced binding of oxytocin in rodents (Arsenijevic, Dreifuss, Vallet, Marguerat, & Tribollet, 1995) and with an increase in cerebrospinal fluid oxytocin levels in lactating adult female rhesus macaques (Parker, Hoffman, Hyde, Cummings, & Maestripieri, 2010), suggesting a potential shift in oxytonergic processing in the aging brain. In further support of age effects on the oxytonergic system, preliminary unpublished data from Ebner's lab suggests that plasma oxytocin levels are lowest in older men compared to women and young adults. Moreover, in both young and older participants, intranasal administration of oxytocin, compared to placebo, results in greater monetary investment in social (i.e., investing into fellow players) compared to non-social (i.e., investing into a computer lottery) trials in the context of a trust game (modified after Baumgartner et al., 2008; see Figure 13.2). We believe that this line of work will be fruitful in further uncovering aging effects in prosociality.

We end this section by emphasizing the necessity for more cross-species work to advance our understanding of complex social cognition in aging. To date, not a great deal is known about how prosocial tendencies of non-human primates change across age. Because non-human primates display remarkably similar social behaviors (Mitani et al., 2012) with largely overlapping functional and structural neural substrates (Chang, Brent et al., 2013; Rushworth, Mars, & Sallet, 2013), research into age-dependent prosocial behaviors and their neurobiological underpinnings in non-humans could supplement already existing and future research on this topic in humans.

Conclusion

In this review of the current literature on prosociality and aging, we have conceptualized prosociality as a multi-faceted phenomenon comprising diverse constructs. We have taken a multi-level perspective that considers a variety of ways in which age-related differences in prosociality can be manifested and organized. With an eye towards developmental trajectories and aging, we have reflected on evolutionary and neural bases of prosociality, as well as prosocial thought and action in the context of specific helper-recipient dyads both in the laboratory and in real-life settings across diverse social contexts.

Current empirical evidence reveals a pattern of stability and even enhancement in affective empathy and related prosocial behavior with aging. This is consistent with Socioemotional Selectivity Theory and the shift from self-oriented future goals to emotionally fulfilling social goals across the adult life span (Carstensen, 2006). However, empathy also requires taking another's perspective (i.e., cognitive empathy), which becomes more difficult with age (Henry et al., 2013). In addition, there is supporting evidence that aging may increase self-reported trust but

decreases trust-sensitivity and that this may be associated with age-related change in attentional processing as well as with age-related neural change.

We hope that this review, and the future research perspectives we have identified, will spur innovative hypotheses and research paradigms to further our understanding of prosociality in aging, a topic with important real-world impact. We see potential for this line of work to clarify pressing societal questions with relevance for individual lives of older adults, not only in avoidance of situations in which they may be taken advantage of, but also in support of conditions under which they are most likely motivated to act prosocially and volunteer their time and resources with maximized benefit to their health and well-being. In closing, thought and action are tied to the environment we live in, and as the environment changes over time, thought and action change as a result. Different periods of the life span may therefore serve as contexts that have a powerful influence over social cognition.

BOX 1 SUGGESTED AVENUES FOR FUTURE RESEARCH IN PROSOCIALITY AND AGING

Variation by Contextual and Interindividual Influences

For example: Investigation of the moderating role of culture, real-life setting versus laboratory context, type of task or game, personality traits, age salience, type of relationship (in-group versus out-group, stranger versus close other, kin relationships)

Determination of Continuous Developmental Trajectories

For example: Incorporation of comprehensive, longitudinal life-span approach comprising middle-aged adult groups, measurement of trust behavior over repeated trust game interactions (versus one-shot interactions) for increased reliability and micro-longitudinal assessment

Neurochemical Basis for the Changes in Prosociality with Aging

For example: Investigation into how various neuromodulators differentially influence prosocial thought and action across aging, including how potentially altered sensitivities engage the neural circuits implicated in social attention and other-regarding decisions

Extension of Direct Cross-Species Comparisons

For example: Examination of humans and non-human primates using tasks and paradigms that are comparable across species to clarify the evolutionary basis and rudimentary mechanisms of prosociality and link it to ontogenesis within the adult life span

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