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A functional MRI study on how oxytocin affects decision making in social dilemmas: Cooperate as long as it pays off, aggress only when you think you can win

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ABSTRACT

We investigate if the neuropeptide oxytocin (OT), known to moderate social behaviour, influences strategic decision making in social dilemmas by facilitating the integration of incentives and social cues. Participants (N = 29) played two economic games with different incentive structures in the fMRI scanner after receiving OT or placebo (following a double blind, within-subject design). Pictures of angry or neutral faces (the social cues) were displayed alongside the game matrices. Consistent with a priori hypotheses based on the modulatory role of OT in mesolimbic dopaminergic brain regions, the results indicate that, compared to placebo, OT significantly increases the activation of the nucleus accumbens during an assurance (coordination) game that rewards mutual cooperation. This increases appetitive motivation so that cooperative behaviour is facilitated for risk averse individuals. OT also significantly attenuates the amygdala, thereby reducing the orienting response to social cues. The corresponding change in behaviour is only apparent in the chicken (or anti-coordination) game, where aggression is incentivized but fatal if the partner also aggresses. Because of this ambiguity, decision making can be improved by additional information, and OT steers decisions in the chicken game in accordance with the valence of the facial cue: aggress when face is neutral; retreat when it is angry. Through its combined influence on amygdala and nucleus accumbens, OT improves the selection of a cooperative or aggressive strategy in function of the best match between the incentives of the game and the social cues present in the decision environment.

1. Introduction

The ability to cooperate *and* aggress is a thumbprint of human nature. But deciding on one or the other when individual interests conflict is not trivial and requires the ability to integrate multiple sources of information at once. How do we do this?

The neuropeptide oxytocin (OT), best known for its hormonal functions facilitating labour and lactation, may have an equally important role as a neurotransmitter in the brain regulating many aspects of human social behaviour that extend beyond reproduction and parental care. Experimental research with intranasal OT administration has revealed a number of ways by which the oxytocinergic system might affect the outcome of social interactions. First, OT stimulates social approach behaviours and strengthens bonds, supposedly because it links social interactions to feelings of reward (Campbell, 2008; Depue and Morrone-Strupinsky, 2005). This is supported by animal research showing that OT stimulates dopamine release in the nucleus accumbens (Dolen et al., 2013), and by neuroimaging studies with humans revealing nucleus accumbens activation when breastfeeding mothers see pictures of their child (Strathearn et al., 2009), or when males in a relationship see pictures of their partners (Scheele et al., 2013). Second, OT is well known to attenuate amygdala activation (Domes et al., 2007a; Kirsch et al., 2005; Labuschagne et al., 2010), removing social anxiety and reducing fear (Heinrichs et al., 2009; Neumann and Landgraf, 2012), which in turn further facilitates social approach (Kemp and Guastella, 2011). Finally, OT may increase the saliency of social cues (Shamay-Tsoory, 2010), which has been corroborated by findings that OT improves performance on theory of mind tasks (Domes et al., 2007b), increases gaze to the eye region of the face (Guastella et al., 2008a), and facilitates finding angry faces in crowds (Guastella et al., 2009), judging the trustworthiness of faces (Lambert et al., 2014), or selecting suitable partners in intergroup conflict (De Dreu et al., 2012).

However, when it comes to predicting the particular social behaviours resulting from intranasal OT administration, experimental research has been contradictory: OT can either decrease (Preckel et al., 2014) or increase social distance (Scheele et al., 2012), encourage defensive behaviours (De Dreu et al., 2015; Striepens et al., 2012) as well as aggression (Campbell, 2008; De Wall et al., 2014), and it can lead to

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cooperation (Arueti et al., 2013) as well as competition (De Dreu, 2012). Taken together, these studies indicate that OT is a moderator of behaviour and that it can have prosocial as well as antisocial consequences, depending on the context and individual differences (Bartz et al., 2011; Declerck et al., 2010; Olff et al., 2013).

To fully grasp the metafunctionality of OT, we need a better understanding of *how* context matters, and what the effects of OT are when there are different sources of information competing for attention. Most experimental studies so far have examined the effects of OT on isolated functions such as perception, social memory, or trust, without considering additional motivational processes that drive moment-to-moment judgments and decision making. Human social behaviour is complex, and key decisions – such as whether to cooperate with or aggress against a stranger – depend on at least two different types of evaluations: first, are there appetitive or aversive stimuli that *incentivize* us to prefer one behaviour over another? And second, are there other salient stimuli that are *informative* about the potential outcome of the behaviour one is about to choose, irrespective of the particular incentives embedded in the decision context. For example, when working in teams, it may be in one's best interest to select a partner with complementary skills (an appetitive stimulus which promises synergy), but in order to prevent being the target of free-riding, it is wise to also consider the potential partner's reputation as a cue of his trustworthiness.

The purpose of the current experiment is to test the proposition that OT helps to integrate these different types of stimuli (incentives and informative social cues) and thereby facilitates ecologically sound decision making in social contexts. Specifically, we propose that OT improves heuristic social decision making, in such a way that we are more likely to select the behaviour (cooperate or aggress) that provides the best match between the incentives and the social cues present in the decision context.

The reasoning behind this proposition is based on OT's interaction with the mesolimbic dopaminergic system (including the ventral tegmental area, amygdala, nucleus accumbens and hippocampus). Recent theories (Love, 2014; Shamay-Tsoory and Abu-Akel, 2015) outline how oxytocinergic neuromodulation of this system can affect *both* incentive motivation *and* the allocation of attention. This is because dopaminergic neurons, originating from two distinct populations in the ventral tegmental area, respond to different properties of stimuli, coding, on the one hand, the *motivational value* of signals in the nucleus accumbens (by strengthening excitatory potentials for appetitive signals, and inhibiting aversive ones) and, on the other hand, the *salience* of signals by activating or attenuating the amygdala (Bromberg-Martin et al., 2010). Through its neuromodulatory properties in the mesocorticolimbic system, OT could bias decision making by means of a two-step process: it influences incentive motivation by strengthening dopaminergic coding of appetitive signals in the nucleus accumbens (see for example Romero-Fernandez et al. (2013)); at the same time, OT-dopamine interactions in the amygdala affect how salient cues (having either a positive or a negative valence) become incorporated in the decision process. Amygdala activation has been associated with vigilance, heightening the orienting response to new, threatening, or unexpected sensory information (Davis and Whalen, 2001). By deactivating the amygdala and strengthening the dopaminergic signal, OT has been proposed to facilitate attention re-orienting (Shamay-Tsoory and Abu-Akel, 2015). Because dopamine neurotransmission is primarily involved in focused attention and action readiness (rather than orienting), OT-dopamine interactions in the amygdala may improve information processing by more accurately responding to the valence of social cue (Tucker and Williamson, 1984). This is a putative mechanism to explain how OT could link the perception of salient social cues to ecologically sound behaviour.

We set up an experiment in which we test if OT can improve the ecological accuracy of complex social decision making through its effects on the nucleus accumbens and amygdala, depending on, respectively, the incentivizing context (appetitive or aversive) and the valence of peripheral social cues (alerting versus neutral cues). To do so, we rely on two economic games to simulate either win-win, or win-lose situations that offer real monetary incentives (see Fig. 1). In an assurance game (AG) the highest pay-off can be obtained by coordinating with one's partner, making cooperation appetitive. The optimal choice in the AG is to cooperate when you believe your partner will cooperate. You also know that your partner has the same incentive to cooperate, which reduces the need to pay attention to other social cues. In contrast, in the chicken game (CG), known as an anti-coordination game, more money can be earned by choosing an aggressive strategy. Here aggression is appetitive, but it is also aversive because all is lost if the partner also aggresses. Thus in the chicken game, the optimal choice is to aggress if you believe you can outcompete your partner, and to back off otherwise. To manipulate the valence of alerting social cues, pictures of angry or neutral faces were displayed on the screen alongside the pay-off matrix of the games, so as to suggest a threatening or safe decision environment. Participants (n = 29) each made 80 decisions in the fMRI scanner after they received OT or placebo (following a double blind, within-subject factor design), in two experimental sessions scheduled one month apart.

Thus, the main goal of the study is to test how OT affects neuromodulation of the nucleus accumbens and the amygdala, two regions of the mesolimbic dopaminergic system that are crucial with respect to incentive-driven behaviour. With respect to the fMRI data, we formulate two specific hypotheses: First, in the AG (the context that rewards mutual cooperation and hence stimulates a win-win outcome), we hypothesize that OT will increase appetitive motivation, and that this will be associated with increased activity in the nucleus accumbens. Conversely, in the more ambiguous CG (signalling a win-lose outcome), aggression is the most desirable outcome, but it is also very risky. Given this ambivalent decision context, OT is expected to inhibit appetitive behaviour and deactivate the nucleus accumbens, relative to the AG. In this case, decision making can be improved by additionally relying on salient social cues. The second hypothesis is that this occurs through a reduction of the orienting response in the amygdala. We therefore expect that OT will attenuate amygdala activation, and that this should be especially apparent when cues are threatening.

With respect to behaviour, we again formulate two hypotheses. First, by inhibiting the orienting response in the amygdala, OT would allow for more accurate encoding of the valence of the cues. This would lead to cue-appropriate behaviour in the CG: if the partner looks too angry, the best decision rule is to back off, especially if losing is fatal. However, if the partner appears neutral and there is a monetary incentive to win, aggressing is the better course of action. This is not expected in the AG where the strong appetitive motivation makes the

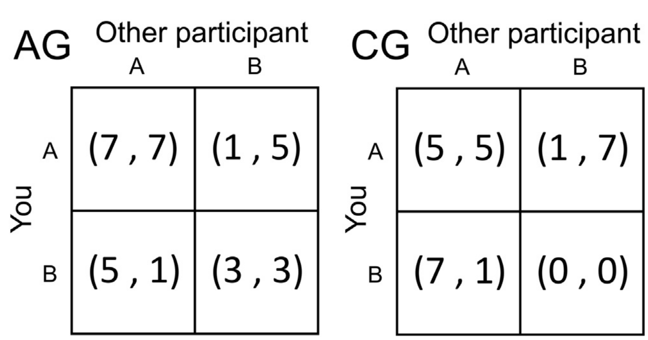

Fig. 1. Example of a pay-off matrix for an assurance game (AG, left panel) and a chicken game (CG, right panel). Each cell depicts the pay-off for yourself and the other participant based on the combination of the chosen options (the first number in the bracket is your outcome, the second one that for the other participant). In an AG, the best outcome is for both to choose A (the cooperative option), yielding 7 euro's each. There is no temptation to earn more by deviating from this choice. This contrasts with the CG, where the highest pay-off is attained when you chose B (the aggressive option) and the other participant choses A (yielding 7 euro's for yourself and 1 for the other). However, if the other also aggresses, both lose everything.