PHILOSOPHICAL TRANSACTIONS B

Review

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The role of self–other distinction in understanding others' mental and emotional states: neurocognitive mechanisms in children and adults

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Social interactions come with the fundamental problem of trying to understand others' mental and affective states while under the overpowering influence of one's own concurrent thoughts and feelings. The ability to distinguish between simultaneous representations of others' current experiences as well as our own is crucial to navigate our complex social environments successfully. The developmental building blocks of this ability and how this is given rise to by functional and structural brain development remains poorly understood. In this review, I outline some of the key findings on the role of self–other distinction in understanding others' mental as well as emotional states in children and adults. I will begin by clarifying the crucial role for self–other distinction in avoiding egocentric attributions of one's own cognitive as well as affective states to others in adults and outline the underlying neural circuitry in overcoming such egocentricity. This will provide the basis for a discussion of the emergence of self–other distinction in early childhood as well as developmental changes therein throughout childhood and into adulthood. I will demonstrate that self–other distinction of cognitive and emotional states is already dissociable early in development. Concomitantly, I will show that processes of self–other distinction in cognitive and affective domains rely on adjacent but distinct neural circuitry each with unique connectivity profiles, presumably related to the nature of the distinction that needs to be made.

1. Introduction

Humans face countless social interactions with friends and strangers on a daily basis. In spite of vast differences between these encounters, the contexts within which they occur and the knowledge available to us about others, we appear to achieve our social goals with apparent ease. Evidence from social psychology and social neuroscience suggests that to understand what others think and feel we rely at least partly on our own projections of what we would think and feel in comparable situations [1,2]. Such claims are buttressed by findings of shared neural representations when thinking about oneself and others or sharing others' feelings [3–5]. While this mechanism works when thoughts and feelings are aligned with one's own, it fails should this not be the case. Therefore, to enable smooth social interactions a distinction has to be made between our own and others' mental representations and emotional experiences. This ability is also known as self–other distinction [6] and has been related to various domains such as perception-action in the form of inhibiting automatic imitation tendencies [7], representing others' mental states that conflict with our own current mental state [6], as well as our ability to empathize with others, particularly when the emotional states between self and other are incongruent [8]. Most of the work understanding the role of self–other distinction in understanding others' mental and emotional states has been carried out in adults. I will therefore begin by summarizing the specific evidence for a role of self–other distinction in these domains, specifically related to the attribution

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of others' mental/cognitive and emotional states in adults henceforth referred to as cognitive and affective self–other distinction, respectively. Behavioural and neurocognitive evidence will be reviewed. This will set the background for understanding the developmental literature on the emergence and development of self–other distinction in childhood. Further, the inclusion of studies in children and adults introduces yet another developmental perspective on the comparability of a role of self–other distinction in child- and adulthood.

2. Inhibiting automatic imitation

A key piece of evidence in the argument for a role of self–other distinction in understanding others' mental and emotional states comes from the use of paradigms in the domain of perception and action. Much like the way our understanding of others' thoughts and feelings relies on projections of our own experiences, the perception of others' actions and the execution of one's own actions are believed to have a common representational basis [9]. Such evidence comes from behavioural findings showing that executing an action will be slowed when simultaneously observing an incongruent action [10]. Further, neuroimaging studies also show that action observation activates brain regions involved in planning and executing actions [11]. According to the most coherent conceptual framework accounting for such shared representation effects, the so-called 'common coding theory' [12], perceivable consequences of actions become associated through learning mechanisms with the underlying motor programme. This in turn constitutes the basis for shared representations for the perception and execution of actions. Importantly, what is not specified by the common code is who caused the corresponding motor representation, i.e. oneself or the other. This can lead to interference when simultaneously performing and observing incongruent actions. To avoid such automatic imitation of observed actions, mechanisms of distinguishing actions produced by oneself and others are required. Such a distinction presumably allows prioritizing the current input in favour of the desired goal of action execution.

The control or inhibition of automatic imitation of others' actions can be used as an index for self–other distinction. Typically, participants are asked to lift their index or middle finger in response to a number, while watching either congruent (i.e. the same) or incongruent (i.e. the opposite) finger movements of a videotaped hand [13]. Whereas in congruent trials the videotaped hand and the instructed movement are identical, in incongruent trials the instructed and observed movements differ. Movements in congruent trials are quasi-imitative leading to faster reaction times, while in incongruent trials such imitative tendencies have to be controlled, leading to slower reaction times. The resulting difference provides a measure for the extent of the interference and makes the degree of self–other distinction in the domain of perception and action measurable.

3. Self–other distinction and others' minds

Our thoughts, beliefs and intentions, in short our mental states, rarely align with those of others. Thus when having to fathom another's mental state, we must avoid merely attributing our own to others. Even though the control problem is converse to that encountered in inhibiting imitative actions, we face a similar challenge in as far as two representations have to be distinguished, in this case our own mental state from that of others [14,15]. This arguably pertains to a whole range of mental states that arise out of experience (i.e. what information does an agent have visual access to and is likely to know as a result versus what do I know as typically tested in visual perspective-taking tasks) as well as beliefs (i.e. what is an agent likely to believe based on their personal experience versus what do I believe as typically tested in paradigms of belief attribution).[1]

The best evidence to date in support of a link between the attribution of mental states and a mechanism of self–other distinction comes from a recent study looking at the effects of training imitation, imitation-control or motor control on a subsequent test of visual perspective-taking [15]. The visual perspective-taking task (also known as the Director's task; [17]) requires participants to take the viewpoint of a 'director' who gives instructions to move objects on a shelf. Experimental trials entail a conflict between the director's and the participant's perspective, explicitly requiring self–other distinction to avoid making errors. Only training imitation inhibition increased participants' performance on experimental trials, an effect that was absent when training either imitation or motor control more generally. This study thus demonstrates that processes of self–other distinction (and not executive functions *per se*, as these would have been targeted by the motor control training) underlie perspective-taking especially when the other's perspective potentially conflicts with our own and mediates our tendency to egocentrically attribute our own states.

4. A specific role for temporo-parietal junction

Evidence that self–other distinction plays a role in the attribution of mental states also comes from the field of neuroimaging. Meta-analyses have shown that the ability to distinguish self-generated actions from externally produced ones relies on some of the same brain region required for mental state attribution, such as the temporo-parietal junction (TPJ; [18]). The TPJ is at the intersection of the posterior end of the superior temporal sulcus, the inferior parietal lobule and the lateral occipital cortex. This region is large and has been shown to have heterogeneous projections depending on sub-regions within the TPJ [19]. Thus parcellating the TPJ based on diffusion-weighted imaging tractography yielded three distinct regions of TPJ, each with unique resting state functional connectivity profiles. Specifically, a posterior TPJ cluster showed greatest connectivity with other brain regions involved in the attribution of mental states, such as the posterior cingulate, the temporal poles and the medial prefrontal cortex [20]. Consistent with the functional specificity of a posterior cluster of TPJ in cognitive self–other distinction, it has been shown that even within the same set of subjects the same part of posterior TPJ is activated for both inhibiting imitative tendencies and attributing mental states [6].

Evidence for a causal role of TPJ supporting self–other distinction to make accurate mental state attributions comes from a recent study using transcranial direct current stimulation (tDCS; [21]). Using excitatory (anodal) as well as

inhibitory (cathodal) stimulation, it was shown that anodal stimulation improved both the control of imitative tendencies (i.e. distinguishing in favour of self-representations) and also improved visual perspective-taking (i.e. distinguishing in favour of other representations). At the same time, social judgements that did not lead to a conflict of self and other representations were left unchanged by tDCS stimulation. While these findings do not speak for a selective involvement of a specific sub-region of the TPJ, they do provide compelling evidence that TPJ is critically involved in self−other distinction, a key process for reducing the effects of egocentricity in social judgements conflicting with one's own mental state.

5. Self−other distinction and others' emotions

As the preceding review illustrates, there is compelling evidence that the *simultaneous* representation of one's own and others mental states relies on processes of self−other distinction, which in turn draws on posterior parts of the TPJ. While this is evidently the case in the context of perspective-taking it still remains unclear whether such a mechanism also operates in the context of emotional state attribution. It has been argued that similar processes underlie the understanding of others emotions, specifically empathic responses [4,18,22]. As a result, for the experience of empathy a distinction needs to be made that the *primary* source of one's feeling is the perception of someone else's experience [23], critically differentiating empathy from emotional contagion. Further, failing to uphold a boundary between self and other when seeing another in pain can lead to feelings of personal distress. Such a self-centred response hinders orienting towards the other and responding empathically, in turn negatively affecting prosocial behaviour [24]. More tentative evidence in support of a role for self−other distinction in empathy comes from a recent meta-analysis showing that empathy, perspective-taking and distinguishing between one's own and others' actions activates the same areas of TPJ [18].

Though paradigms on empathic responses typically measure the extent to which we share the feelings of another when we are in an otherwise neutral state, processes of self−other distinction might not necessarily be required. A better way of testing for a potential role of self−other distinction in understanding others' feelings would be through the induction of feelings congruent or incongruent to another. Precisely such a design was deployed by means of affective visuo-tactile stimulation [8]. Participants were invited in pairs and underwent separate but simultaneous stimulation through two experimenters. Stimulation was performed such that participants were touched with material of either positive or negative valence while seeing at the same time a depiction of what they were stimulated with as well as what stimulation the other participant was currently undergoing. This way it was possible to create affectively congruent (i.e. both participants received positive or negative touch) or incongruent experiences (i.e. one participant received negative touch while the other received positive touch and vice versa). After each trial, participants were asked to either rate how they themselves felt or how they thought the other felt. Using this procedure, it was possible to assess the extent to which participants might be egocentrically biased in their attribution of emotional states. Such a bias should manifest itself through stronger attributions of emotions to others when these are congruent with one's own states compared to when they are incongruent. Exactly such an emotional egocentricity bias was found. Thus in a paradigm analogous to perspective-taking studies, it was shown that egocentricity occurs also in the affective domain.

6. A specific role for right supramarginal gyrus

Do processes of self−other distinction required to overcome emotional egocentricity rely on the same brain regions as those relied on to overcome cognitive egocentricity? In two functional magnetic resonance imaging (fMRI) studies, it was found that temporo-parietal areas were activated [8]. The activations were not part of the more posterior cluster typically found for the attribution of mental states however, but rather located more anteriorly, comprising a brain region also known as the supramarginal gyrus (SMG). An overlap of brain regions involved in perspective-taking showed that these were anatomically distinct clusters. Evidence in favour of right (r) SMG subserving mechanisms of self−other distinction was indicated by findings of increased emotional egocentricity after performing low-frequency repetitive transcranial magnetic stimulation (rTMS) over temporo-parietal regions compared with sham stimulation.[2] This suggests that whereas temporo-parietal regions might overall be functionally involved in self−other distinction, precisely which part is recruited will depend on the nature of the distinction made (i.e. motor, cognitive or affective). One reason for this could be distinct connectivity profiles of subregions of TPJ, which might make posterior regions more suited for self−other distinction in the cognitive, and anterior regions more suited for such computations in the affective domain. The findings by Mars *et al.* [19] already indicate that posterior rTPJ is intrinsically more connected to brain regions involved in mental state attribution and perspective-taking (i.e. posterior cingulate, temporal poles and medial prefrontal cortex [20]), whereas anterior portions, corresponding to the rSMG, show stronger intrinsic connectivity to brain regions implicated in empathic responses (i.e. anterior insula, anterior cingulate cortex [4,25]). Such a functional distinction was confirmed more recently using seeds derived from activations in the context of overcoming emotional egocentricity [26,27]. This suggests a functional differentiation in temporo-parietal areas in terms of their role of self−other distinction in different social domains.

7. Interim summary

In sum, mechanisms of self−other distinction appear to play a crucial role in the context of understanding others' mental as well as affective states. This is supported by evidence of improvements in perspective-taking following training the inhibition of imitative tendencies on the one hand as well as findings of a strong effect of one's own emotional experience on judgements of others' emotional states. While such mechanisms both recruit temporo-parietal brain areas when needed to overcome cognitive and affective egocentricity; in each case different subregions are activated. Thus, more posterior parts of TPJ are relevant for overcoming cognitive

egocentricity; anterior parts of TPJ, specifically rSMG, perform such a function for overcoming affective egocentricity. Presumably each of these subregions are uniquely suited to overcome egocentricity in these respective domains as a function of their intrinsic connectivity with brain regions involved in attributing mental and affective states, respectively.[3] Given that these temporo-parietal regions are among the latest of the cortex to mature [29], such a protracted developmental process might also relate to the development of self–other distinction and its role in understanding others' mental and emotional states.

8. Development of self–other distinction

The ability to distinguish between self and other presupposes having a concept of self and a concept of another. When does this emerge in childhood? Early studies on infant imitation have shown that neonates already appear to have a tendency to automatically imitate others' actions [30], providing a tool to learn about others' mental and emotional states (but see [31] for a critical discussion). In turn, it has been shown that neonates seem to distinguish their own actions from externally produced ones as indicated by differences in facial microexpressions [32]. This however may not constitute a full-fledged concept of self, which has been proposed to emerge during the first years of childhood when children pass the so-called mirror self-recognition test at 18 months [33].[4] Such an ability has been shown to emerge with self-conscious emotions such as embarrassment [34], which is why it is believed that by the age of 18 months children have developed a concept of self. The age at which children acquire a concept or theory of other minds is a much more contentious issue and is, largely due to the methodologies employed, intricately linked to the question of development of self–other distinction. In this section, the literature on both of these will be discussed.

(a) Cognitive self–other distinction
(i) Emergence
One of the most studied phenomena in social development is when children reliably attribute mental states to others. This pertains to their ability to appreciate that someone looking at the same object but from a different angle might see it differently (i.e. level 2 perspective-taking) as well as attributing beliefs to others. The classic measure for assessing belief attribution is the so-called false-belief test [35,36]. Proposed as the best assessment of a child's theory of mind [37] are tests tapping the ability to attribute a belief accurately to another agent even when this conflicts with reality and the child's own beliefs. It has been shown that whereas 3-year-olds typically fail such tasks, most children pass by 4 years [38]. Passing this task is seen as a fundamental shift in children's understanding of others between the ages of 3 and 4 years [39,40] in that they build a representation of others' mental states which can differ from their own.[5]

Whereas passing such a test is taken as an indicator of the child's representation of another's perspective, such false-belief tests also perfectly exemplify the kind of self–other distinction required for accurate perspective-taking to take place in that children need to inhibit attributing their own belief, which is incongruent to the agent's whose belief they in turn need to predict.

One crucial question is however if children may not have acquired a theory of mind prior to passing explicit false-belief tests. Explicit false-belief tests have been criticized partly because they rely on well-developed language skills as well as executive functions, abilities which also develop between the ages of 3 and 4 years [43]. Such task-related demands may mask the underlying abilities that for instance infants might possess [44]. Using false-belief tasks that do not explicitly refer to the belief context (and thus avoid confounding this with mastery of language and level of executive functions) when asking for responses, it has been shown that infants already in their second year of life pass non-verbal false-belief tests [44,45].[6] This would mean that passing a false-belief test around 4 years is more a test of how well mechanisms of self–other distinction are in place as opposed to whether the child can represent another's mental state. However, findings of an early theory of mind have been questioned as to whether they really reflect an infant's access to another's belief as opposed to relying on basic behavioural cues [47] or effects of novelty biasing responses [48]. Thus, depending on whether evidence in favour of early forms of theory of mind holds up against current criticisms, passing false-belief tests around the age of 4 years reflects a critical developmental step in terms of self–other distinction and perhaps also the acquisition of a theory of mind.

So far, imaging studies that capture this crucial developmental period are lacking. However, our group has recently conducted a cross-sectional study of children aged 3–4 years. Children were given classic false-belief tasks and measures of structural brain development were also obtained. In a tract-based statistics analysis, it was found that white matter development in the right TPJ correlated with false-belief understanding [49]. Whereas it is still unclear whether this brain region is also relevant during actual task-performance, these data underscore a crucial relevance of right TPJ for the observed developmental transition between 3 and 4 years in successfully passing false-belief tests. Earlier studies provide indirect evidence which corroborate our conclusion [50]. Thus, Sabbagh et al. [50] measured amplitude and coherence from resting state electroencephalograms and linked this with performance on a false-belief task in 4-year-olds. They showed that current density of alpha waves in right TPJ (and dorsomedial prefrontal cortex) correlated best with individual performance in false-belief tasks. Both studies suggest that the structural maturation of rTPJ is critical for self–other distinction in perspective-taking to arise, which leads to a leap in reduced cognitive egocentricity in children.

(ii) Development
The nature of developmental change of self–other distinction throughout childhood is still a matter of debate. For instance, the so-called pure-conceptual change accounts [40,51] and the executive emergence accounts [52] would argue that once the necessary concepts of other minds are in place (i.e. either through the acquisition of concepts or the emergence of executive functions enabling the emergence of theory of mind concepts) perspective-taking should be mastered no matter how demanding. Alternatively, the so-called executive performance accounts predict that as long as a need for inhibition is required then perspective-taking ought to continue being taxing in development but increasingly less so [53,54]. In a recent study looking at belief-desire reasoning

in children aged 6–11 years (and thus long able to pass standard false-belief tests), it was found that younger children had greater difficulty attributing beliefs and desires to an agent as indicated by slower reaction times and greater errors, which decreased with age [55]. However, there were no developmental changes in the difference between attributing true and false beliefs in reaction time or errors. Thus, when the demand for self–other distinction is greater, as is the case for false beliefs compared to true beliefs, this seems to be found equally difficult under the presented task demands. A similar absence of a developmental decrease in egocentricity is echoed in a study on visual perspective-taking [56]. While some studies using the belief-desire reason task found clear age-related changes [26] others report persistent changes in visual perspective-taking throughout adolescence [57]. The most parsimonious account to explain these developmental patterns is in fact one of demands placed on executive functions by the task. As executive functions are also relevant for theory of mind performance in children [52], given that executive functions develop considerably throughout childhood [58], this ability will interact with the necessity for concurrent distinction made between self and other. In sum, self–other distinction is hindered or helped by the extent to which tasks demand more or less executive functions, which in turn are sensitive to developmental changes.

(b) Affective self–other distinction
(i) Emergence
As outlined above, it has been argued that understanding others' emotional states, also known as empathy, requires a form of self–other distinction [4,18,59]. The best empirical evidence for this actually comes from developmental psychology. In a seminal paper, Bischof-Köhler [60] made such a link explicit by giving children aged 16–24 months a mirror self-recognition test and observing their emotional and behavioural responses to the plight of a confederate adult (confederate cries in response to her teddy's arm breaking off; see also [61]). She shows that the children passing the mirror self-recognition test (and thus with a mature concept of self and presumably capable of making the distinction between self and others) were also significantly more likely to help the confederate (i.e. comforting; attempts to repair teddy). To date, this study is one of the few pieces of evidence which actually demonstrates the crucial role of self–other distinction in bringing about empathic responses.

(ii) Development
Apart from a potential role of self–other distinction in producing the shift from emotional contagion to empathic responses, such a process would be even more necessary when bringing about accurate empathic judgements when the other's state differs from one's own (like in the study by Silani et al. [8]). To test for developmental changes in this ability, we conducted a study with children ranging from 6 to 13 years of age as well as adults using monetary rewards and punishments to induce positive and negative affective states [26]. Like in the previous study by Silani et al. [8], participants were made to feel either congruent or incongruent to one another and asked to rate how they thought the other felt. Two particular age-trends emerged: while overall affective egocentricity declined throughout childhood, adults were

also less egocentric than children overall. Importantly, both of these findings could be independently replicated using a new paradigm inducing emotions by means of pleasant and unpleasant gustatory stimulation (i.e. sweetened water/juice and saline/quinine solutions, respectively; [62]). Crucially, the study by Hoffmann et al. [62] could show that the developmental decrease in affective egocentricity was critically mediated by resolving conflict between two concurrent emotional representations, which is precisely the sort of computation subserved by self–other distinction. Thus, self–other distinction required for overcoming affective egocentricity increased significantly both throughout childhood as well as into adulthood. Importantly, both studies included several measures of cognitive perspective-taking. While these were also shown to change significantly with age there were no correlations between emotional egocentricity and cognitive perspective-taking, suggesting that at the behavioural level self–other distinction in the cognitive and the affective domains are dissociable in development.

Using neuroimaging, Steinbeis et al. [26] investigated the neurocognitive mechanisms underlying this developmental effect. Children showed significantly reduced activity of the rSMG compared with adults and this activation difference overlapped with the rSMG activation in the study by Silani et al. [8]. Further, the smaller the affective egocentricity the stronger the functional connectivity between rSMG and left dorsolateral prefrontal cortex (DLPFC), but only in adults and not in children. These data suggest that children are affectively more egocentric than adults as a result of poorer affective self–other distinction, in turn due to the prolonged maturation of the relevant brain regions such as rSMG. We also established by means of performing a functional resting-state analysis of seeds in the rTPJ and rSMG that in children the distinct networks of increased connectivity with brain regions involved in mental state and affective state attribution, respectively, are already present and comparable to adults. This suggests a functional specificity of both rTPJ and rSMG in children as young as 6 years that makes each of these brain regions particularly suited to performing computations of self–other distinction in the cognitive and the affective domain, respectively. At the same time, however, it appears that the recruitment of these regions when actually having to perform the computations requires further functional maturation [26,63].

9. Conclusion
This review presented evidence suggesting a crucial role of self–other distinction in understanding others' mental and emotional states in adults as well as in children, particularly when these states are in conflict with our own. Further, self–other distinction appears to be differentiated between cognitive and affective domains. This is supported by a lack of correlations in tasks requiring self–other distinction at the behavioural level as well as distinct neural correlates for each. In adults as well as in children there is good evidence to suggest that even though cognitive and affective self–other distinction rely on temporo-parietal brain regions, they rely on distinct sub-regions, namely posterior TPJ and SMG, respectively. One reason for this differential recruitment of distinct sub-regions of temporo-parietal cortex could be the intrinsic functional connectivity of TPJ and SMG. Thus, TPJ

is more connected to brain regions involved in attributing mental states, whereas SMG is more connected to regions involved in attributing affective states, a pattern already present in childhood. In sum, self–other distinction is a crucial mechanism for overcoming egocentricity across experiential domains, which is subserved by specific brain regions, a specification that unfolds early in child development.

Endnotes

[1]The attribution of one's own mental state to others could occur also from disregarding the other's state and automatically attributing one's own, as opposed to a lack of self-other distinction. However, evidence on the automaticity of adopting the perspective of another even when this is not required suggest that some representation of what others know or feel is invariably computed [16] and will have to be navigated.
[2]Note that even though the regional specificity of rTMS is too imprecise to say with any certainty that only rSMG was affected, and in turn leading to increased emotional egocentricity, the fact that only rSMG (and not rTPJ) was activated in the fMRI studies makes it reasonable to assume that only the disruption of brain regions functionally implicated would lead to such an increase in emotional egocentricity.
[3]Interestingly, a recent study has shown that psychosocial stress can lead to comparable detriments across motor, cognitive and affective domains as indicated by a reduction in imitation control as well as greater cognitive and affective egocentricity [28]. While this tells us little about the underlying mechanisms, it shows that social contexts can have a global effect on self-other distinction across domains.
[4]Children are surreptitiously marked with red paint on their face and placed in front of a mirror. Touching the mark on their face is interpreted as a sign of self-recognition.
[5]Interestingly, a study on the attribution of desires shows that children can reliably attribute a desire to others incongruent to their own from around 18 months [41]. Some see this as evidence for the fundamentally different nature of belief attribution compared with other states [42].
[6]More recently, it has been shown that infants as young as seven months automatically compute what an agent can and cannot know by looking longer at events that an agent would not have expected even when the event conforms to the infant's expectations [46].

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