



How does the 'rest-self overlap' mediate the qualitative and automatic features of self-reference?

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Discussion Paper

Attentional control and the self: The Self-Attention Network (SAN)

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Although there is strong evidence that human decision-making is frequently self-biased, it remains unclear whether self-biases mediate attention. Here we review evidence on the relations between self-bias effects in decision-making and attention. We ask: Does self-related information capture attention? Do self-biases modulate pre-attentive processes or do they depend on attentional resources being available? We review work on (1) own-name effects, (2) own-face effects, and (3) self-biases in associative matching. We argue that self-related information does have a differential impact on the allocation of attention and that it can alter the saliency of a stimulus in a manner that mimics the effects of perceptual-saliency. However, there is also evidence that self-biases depend on the availability of attentional resources and attentional expectancies for upcoming stimuli. We propose a new processing framework, the Self-Attention Network (SAN), in which neural circuits responding to self-related stimuli interact with circuits supporting attentional control, to determine our emergent behavior. We also discuss how these-bias effects may extend beyond the self to be modulated by the broader social context—for example, by cultural experience, by an in-group as opposed to an out-group stimulus, and by whether we are engaged in joint actions. Self-biases on attention are modulated by social context.

Keywords: Self-bias; Attention; Own-name effect; Own-face effect.

There is a growing literature demonstrating that human decision-making is biased toward the self. For example, our memory for self-related material is typically better than for material related to other people (Conway, 2005; Conway & Pleydell-Pearce, 2000; Cunningham, Turk, Macdonald, & Neil Macrae, 2008). There are also effects on perceptual judgments. Thus, the time to decide whether a face is oriented to one side or not is affected by whether it is the participant's own face—orientation judgments are faster to our own face than to other's faces (Keyes & Dlugokencka, 2014; Sui & Han, 2007). Self-relevance even

affects simple perceptual matching of shapes and labels. After being told to associate a shape with a label, participants are quicker and more accurate at deciding that shape-label pairs are associated if the pair relates to the participant's own identity (circle-you) than if the pair relates to another person (square-best friend) (Sui, He, & Humphreys, 2012). Furthermore, matching responses to self-related stimuli are less affected by reductions in the contrast of the shape than are match responses to other stimuli (Sui et al., 2012)—a result consistent with the self-bias modulating perceptual processing of the shape.

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In these studies of self-bias on memory and perception, the stimuli have typically been presented at attended locations (e.g., at the center of the visual field) and they have been task relevant. Hence, it is not clear how these self-biases relate to attention. Are self-biases dependent on attention or can self-relatedness be computed pre-attentively? Is attention attracted to self-related information? The aim of this review is to evaluate these questions, drawing on evidence from studies using a range of different experimental paradigms and three different types of stimuli which have been frequently used (own names, faces, and self-associated shapes). We organize the review by the different experimental effects that have been employed, asking whether common conclusions can be drawn across the different stimuli and procedures. We use both behavioral and neural evidence to motivate a new framework for understanding the relations between attentional control processes and the self: The Self-Attention Network (SAN). We also discuss how the framework may be extended to incorporate in-group biases in perception and the relations between attention and joint action.

THE OWN-NAME EFFECT

Probably the most long-standing argument that self-biases can modulate attention comes from studies of the “own name effect.” Moray (1959) presented names in the unattended ear as participants engaged in shadowing the contents of the other ear. After carrying out the task, participants were asked whether they could recall any stimuli on the unattended ear. Moray found that participants were better able to report words in an unattended ear when they followed the presentation of the participant’s own name, compared with the names of other people. This classic result has been taken to suggest that self-relevance can be computed even when stimuli are unattended, and that it then modulates attention (e.g., attracting attention to the unattended ear). That is, self-relatedness can be computed pre-attentively.

There are several ways in which the result could be accounted for, but one (Treisman, 1960) is that stored representations of our own names have a reduced threshold for being activated by incoming stimuli. Unattended stimuli may undergo some processing pre-attentively, but at an attenuated level, compared with when stimuli are attended. The reduced threshold for our own names, however, means that, even when processing is attenuated, it may still be sufficient to exceed a threshold for awareness—with

the result that stimuli conforming to one’s own name enter awareness and attract attention. However, there are alternative views. For example, it may be that even when carrying out a shadowing task, participants occasionally switch attention to the unattended channel, enabling stimuli occurring there to be attended (see Lachter, Forster, & Ruthruff, 2004). The enhanced report of own-name stimuli may then reflect (perhaps) a bias to respond to these names compared with other names—not an effect based on unattended processing of own names that subsequently cue attention.

Since Moray’s pioneering work, a large number of studies have shown robust support for the preferential processing of own-name stimuli, even in six-month-old infants (Imafuku, Hakuno, Uchida-Ota, Yamamoto, & Minagawa, 2014). The exact relation of the phenomenon to attention, however, is controversial. There is certainly evidence indicating that one’s own name can be processed automatically to affect ongoing task performance. For example, the central presentation of your own name can disrupt the detection of peripheral stimuli (Bargh & Pratto, 1986; Wood & Cowan, 1995) and hearing your own name in an irrelevant list can reduce working memory capacity (Röer, Bell, & Buchner, 2013). Bundesen, Kyllingsbark, Houmann, and Jensen (1997) reported that there was a reduced “attentional blink” on own-name stimuli,¹ consistent with own-name stimuli being better able to survive when attention is limited. In addition, own names are less subject to “inattentive blindness”² (Mack & Rock, 1998) and to “repetition blindness”³ (Arnell, Shapiro, & Sorensen, 1999). Yang, Wang, Gu, Gao, and Zhao (2013) have also reported that, in visual search, participants fixate earlier and make fewer saccades when the target is their own name compared with the names of others.

Other data, though, do not tell such a simple story. Like Yang et al. (2013), Harris, Pashler, and Coburn (2004) reported more efficient visual search for own name relative to other name targets, but, perhaps more crucially, search never became so efficient that targets

¹The “attentional blink” is the term used to describe the relatively poor report of a second target if it appears after a first reported target. It is thought to reflect a limitation in attentional rather than perceptual processing because the second target can be identified if the earlier target has to be ignored (Raymond, Shapiro, & Arnell, 1992).

²Inattentive blindness occurs when participants fail to notice stimuli that are unexpected in the context of the experiment, although perfectly visible (Mack & Rock, 1998).

³Repetition blindness arises when participants fail to notice a second, repeated presentation of a stimulus (Kanwisher, 1987).

could be said to “pop out.” That is, the own-name advantage may depend on some attention being allocated to stimuli, as participants search a display. Other investigators have reported that the own-name effect decreases when stimuli are presented outside the focus of attention (Bundesen et al., 1997; Devue & Brédart, 2008). For example, Bundesen et al. (1997) briefly presented words in one of two colors and required participants to report items from one but not the other color. Having the participant’s own name in the distractor color did not disrupt performance. Harris and Pashler (2004) did report differential distraction from own name compared with other names, but only when the own names appeared as rare events. They had participants make parity judgments to pairs of numbers that flanked distractor words. Presenting the participant’s own name as a distractor disrupted search when the own name appeared on a minority of trials, but this effect disappeared if the own-name distractors occurred half the time. Rather than reflecting automatic attention capture by one’s own name, these data may reflect the surprise of occasionally seeing your own name on trials where the distractor is attended. Converging evidence using event-related responses shows that hearing and/or seeing one’s own name is associated with an enhanced P300 component (e.g., Eichenlaub, Ruby, & Morlet, 2012; Tacikowski, Cygan, & Nowicka, 2014). Although the P300 has been linked to attentional processes, it is also a relatively late component, suggesting that own-name effects do not necessarily reflect the first capture of attention by the stimulus (though see Fan et al., 2013, for evidence of some effects on earlier ERP components).

Despite the negative results we have noted, recent studies do suggest that, at least under some circumstances, the presence of one’s own name can cue attention, the effect is automatic and can still arise when words are presented too briefly to discriminate. Alexopoulos et al. (2012) presented names as cues prior to a visual search display (an O target had to be detected amongst Q distractors). Presenting an own name at the target location facilitated search. This occurred even when the words were masked so that participants could not judge if the word was their name or not. Moreover, in an “antisaccade” version of the procedure, the word cue always appeared on the opposite side of fixation to the target so that participants should try to make a saccade away rather than toward the cue. In this case, the own name disrupted performance, suggesting that participants found it difficult not to attend to the stimulus. We note, however, that these results occurred under conditions in which only a single

cue stimulus appeared in the display and participants likely adopted a distributed mode of attention for the subsequent search task. The data suggest that one’s own name can be a potent signal for attention, but perhaps only under conditions where there are sufficient attentional resources for processing.

Gronau, Cohen, and Ben-Shakhar (2003) examined the relations between the own-name effect and the attentional focus by having participants name central color stimuli. In one case the colors fell on a central word (which could be the participant’s own name) and in a second case there was a central color patch flanked by a word. When the word was presented centrally, color-naming was disrupted by the presence of the participant’s own name, compared with other names. However, this behavioral effect disappeared when the word was not attended. The data suggest that there needs to be some allocation of attentional resource for the participant’s own name to disrupt ongoing performance. Interestingly, however, the authors also measured galvanic skin responses and found enhanced effects for own-name compared with other stimuli, even when the own name was presented peripherally. It may be then, that names need to be attended in order to break into awareness and direct attention, but there can nevertheless be some implicit processing without awareness.

These effects with own-name stimuli could reflect several properties of the items—that your own name relates directly to your self-representation, that it has high emotional significance or reward value (Northoff & Hayes, 2011) or, that it is based upon the familiarity of your own name compared with the names of other people. The effects of familiarity may be better teased apart when stimuli other than one’s own name are used—such as your own face, or even an arbitrarily associated stimulus. It is to studies with these stimuli that we now turn.

OWN-FACE BIAS

Alongside studies of the own-name effect, there is a body of evidence examining self-related biases in face processing. As noted above, participants are faster and more accurate at making perceptual judgments about the orientation of faces if they see their own face compared with the faces of other people (Keyes & Dlugokencka, 2014; Ma & Han, 2010; Sui & Han, 2007). Perhaps more than the own-name effect, this own-face advantage is associated with relatively early components of the visual evoked response, which are typically thought to reflect either enhanced perceptual processing or enhanced allocation of attention to

stimuli. For example, Sui, Zhu, and Han (2006) reported that self-faces generate increased positivity over frontal-central regions within a time window 220–270 ms post stimulus onset (the anterior N2). Moreover, this effect on ERPs remained even when participants made a discrimination on a central cross and the faces were presented as distractors—when there can be behavioral disruption by a self image compared with the face of another person (Brédart, Delchambre, & Laureys, 2006). Caharel et al. (2002) similarly reported a reduced P2 component (around 250 ms post stimulus onset) for the contrast between the participant’s own face and a familiar other face, and Keyes, Brady, Reilly, and Foxe (2010) report an enhanced N170 component to the self-face versus the face of a friend. Such results suggest that our own face can evoke a relatively rapid attention-related response, and this can arise even when the faces are not task related.

Some authors have argued that this self-face effect may be driven by a link between self-related stimuli and positive self-evaluation—reflecting a socio-cognitive mechanism in self processing (Ma & Han, 2010). In contrast to this interpretation of high-level processing, Sui and Humphreys (2013) proposed an interpretation at the perceptual level in which the self-advantage effect in face processing results from participants using the self-other distinction as a basic anchor-point in the perceptual categorization of faces. Sui and Humphreys showed that the distribution of response times to self-faces did not vary as decision boundaries varied (categorizing self vs. friend + stranger, or self + friend vs. stranger), whereas there were shifts in the response distributions to other faces.

The study of Sui and Humphreys (2013) indicated that responses to a friend’s face varied across categorization tasks as did responses to the face of a stranger, suggesting a qualitative distinction between the processing of self-faces and other faces. Given that a friend’s face will be highly familiar relative to the face of a stranger, then the self-face advantage cannot easily be attributed to (at least linear) effects of familiarity.

There are also data indicating that the self-face can cue attention. Liu, He, Rotshtein, and Sui (this issue) used self- or other-faces as a central cue prior to a peripheral letter target. The face changed its orientation dynamically so that it turned either to the location where the target would appear (on valid trials) or to a homolog location on the opposite side (on invalid trials). Liu et al. found that the self-face acted as a stronger attentional cue than the faces of other people, particularly when there was a short interval between the cue and the target. Moreover, the onset of the self-

face elicited a larger N1 (an early attention-related component) compared with other faces. Interestingly, the magnitude of the N1 effect correlated with self-other differences in the P300. Apparently the early attentional effect of the self-face also modulated later attention-related processes, perhaps concerned with decision certainty about the stimulus.

Other investigators have provided some evidence the own-face effect can occur even when participants are not aware of the stimuli. For example, Tao, Zhang, Li, and Geng (2012) used continuous flash suppression to minimize awareness for faces. The suppressed faces were followed by words and the task was to decide if the word had a positive or negative valence. Despite participants being unaware of the face, participants with high self-esteem responded faster to positive words when the words were preceded by their own face compared with the face of another person.

However, not all the evidence fits with there being automatic processing of self-faces. Keyes and Dlugokencka (2014) presented participants with faces and names, with the task being to name the word. The word could appear on a centrally presented face (falling at the focus of attention) or the word could be flanked by peripheral faces. When the face fell at the focus of attention, self and friend naming was facilitated by a consistent face. However, this effect disappeared when the face fell at a peripheral location. The data suggest that the own-face effect, similar to the own-name effect, may be dependent on the presence of some attentional resource being allocated to the locations where stimuli fall. This may be the case even when the stimuli are subsequently masked so that they are not available for conscious report (cf. Tao et al., 2012).

SHAPE PERCEPTION

Although studies of the own-face effect are perhaps less confounded by effects of familiarity than studies of the own-name effect, it remains difficult to eliminate the possibility that our own faces are more familiar than the faces of other people. The question of whether self-related stimuli are in some way “special,” or whether they simply reflect a far point along a continuum of familiarity cannot be laid to rest. This issue can be set aside when self-association effects are considered. Sui et al. (2012) introduced a new paradigm for studying self-bias based on a simple associative matching procedure. Participants were asked to form associations between labels referring to different people and a shape. For example, they might be asked

to associate a circle with the label “you,” a square with the label “friend” and a triangle with the label “stranger.” Following this, participants saw shape-label pairs which were either the original pairings (circle-you, square-friend, triangle-stranger) or re-paired stimuli (circle-friend, square-stranger, triangle-you). The task was to decide whether the stimuli were the original pairing or whether the shapes and labels had been re-paired. A substantial advantage occurred for matching self-related pairs over the pairings of other stimuli. This advantage occurred even when participants carried out sequential matching in which the label preceded the shape, when responses were made only to the formerly neutral shapes, minimizing differential effects of the familiarity of the imperative stimulus. The effect was also independent of factors such as the frequency or concreteness of the label.

Sui, Sun, Peng, and Humphreys (2014) evaluated whether the self-advantage following associative learning occurred automatically or whether it was contingent on participants forming expectations for self-related stimuli. To assess the automaticity of the effect, Sui et al. varied the probability with which different pairings occurred. Sui et al. also compared self-associations with associations referring to the participant’s mother, a highly familiar other, as well as associations to a stranger. Within different experiments two of the associations had a high frequency of occurrence and the other association appeared on a low frequency of trials. Reducing the frequency of occurrence of the mother and stranger associations slowed RTs to these stimuli, compared with when the self, mother, and stranger associations had an equal probability of occurring. In contrast, there was no cost to matching self-associated items when they became low-frequency events. This is consistent with the self-advantage occurring automatically, even when self-stimuli are not expected.

In addition to this, Sui et al. (2014) found that increasing the probability of the different pairings facilitated responses to all stimuli, compared with when the pairings had equal probabilities of occurrence. This fits with processing being enhanced when there is a top-down expectation for particular pairings. Interestingly, this top-down effect was also modulated by self-bias. When the mother and stranger associations both had a high probability of occurrence, performance improved for both pairings (compared with the equal probability baseline), suggesting that two expectations were maintained. However, when the self-associated stimuli had a high probability of occurrence along with either the mother or the stranger association, there was a benefit *only* for the self-related items. This result indicates

that, when they had a high frequency of occurrence, self-related items were differentially weighted in any expectancy, minimizing any benefits for other high-frequency stimuli. Illustrative results are presented in Figure 1. That is, as well as there being an automatic component to the self-bias effect, there was a further component based on differential expectancies for the self versus other people.

The neural basis of these self-association effects were examined by Sui, Rotshtein, and Humphreys (2013) using fMRI. They found that match responses to self-related stimuli were associated with enhanced neural activity in two regions: The ventro-medial pre-frontal cortex (vmPFC) and the left posterior, superior temporal sulcus (LpSTS). The vmPFC has previously been associated with self-biases in a range of tasks, including memory and trait judgements (Jenkins & Mitchell, 2011) and it has been proposed that this brain region is the seat of our self-representation (Lieberman, 2007). In contrast, the LpSTS has been linked with social attention to our environment (Allison, Puce, & McCarthy, 2000; DiQuattro & Geng, 2011; Saxe & Kanwisher, 2003). Dynamic causal modeling of the data (Penny et al., 2010) suggested that enhanced responses to self-related stimuli were associated with strong top-down connections from the vmPFC to the LpSTS, consistent with the idea that early activation of self-representations primes the attentional system to respond to self-related stimuli (cf. Chaumon, Kveraga, Barrett, & Bar, 2014). Interestingly, the opposite contrasts (where there was greater activity for shape-label matching to the stranger and the friend) were associated with activation of the fronto-parietal network associated with attentional control (Corbetta & Shulman, 2002). The neural circuitry fits with the idea that there may be responses to self-related stimuli that are independent of the attentional control network, with the attentional control network being recruited in order to make the more difficult associations (e.g., between a shape and a label for a stranger).

These arguments for contrasting roles of a self-related network and an attentional control network are supported by emerging neuropsychological evidence. Sui, Enock, Ralph, and Humphreys (in press) reported data from patients with lesions that included: vmPFC, LpSTS and the fronto-parietal attentional network. Damage to the vmPFC led to a hypo-self response in which self-biases (e.g., in associative matching but also in memory) were eliminated, and so differed from the positive biases found in normal participants. In contrast, damage to the LpSTS led to a hyper-self-bias effect. This was attributed to a reduced ability to modulate social

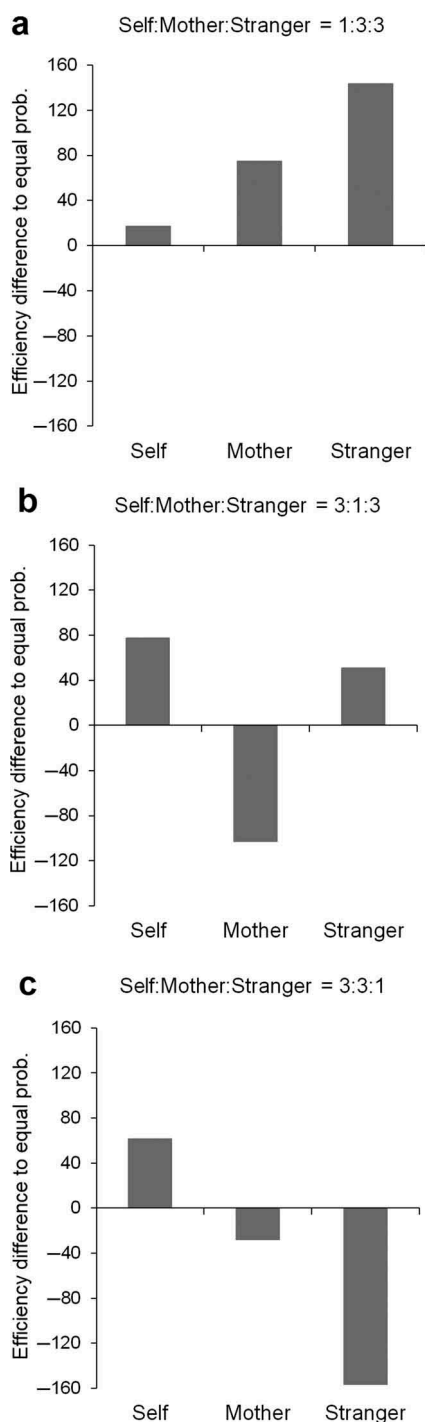


Figure 1. Response efficiency (RT/proportion correct responses) to self-, mother-, and stranger-related stimuli as a function of the frequency with which matching trials for the stimuli occurred within a trial block. The data are plotted here relative to a baseline condition in which the different stimuli appeared with equal probability. A positive number indicates that performance was more efficient with mixed than equal probabilities. A negative number indicates that performance was less efficient with mixed than equal probabilities (Sui et al., 2014).

attentional responses through the LpSTS in the presence of a strong driver of social attention (self-related stimuli). In addition to this, damage to the fronto-parietal attentional control network was also linked to hyper-self-biases. Here we propose that patients with lesions of the attentional control network lack sufficient attentional resources to make efficient matches to the more difficult associations (shape-label associations for the stranger) but the reduction in attentional control does not impact on the strong responses to self-related stimuli. Sui et al. (in press) suggest that these different neural circuits will typically interact to determine performance. For example, when there is strong but irrelevant self-related activity acting to “drive” attention (e.g., operating through the vmPFC and LpSTS), then the attentional control network must work more strongly to overcome a bias to respond which (for example) could disrupt the ability to reject mismatching stimuli when a self-associated item is a member of the pair. Similarly, the attentional control network may need to be engaged to some degree to ensure that there is sufficient bottom-up activation of the self-related network, in the first place (cf. Gronau et al., 2003; Keyes & Dlugokencka, 2014).

This argument, for the recruitment of an attentional control network to modulate self-related distraction is supported by both behavioral and functional neuroimaging evidence. Sui, Liu, Mevorach, and Humphreys (2013) examined the relations between the functional and neural responses to self-associated stimuli and those to stimuli varying in perceptual saliency, in tasks requiring selection between target and distractor shapes. They had participants first form associations between shapes and self, friend, and stranger labels. Subsequently, they presented hierarchical (local-global) forms made up of either the self and stranger shapes, or the friend and stranger shapes. Participants were cued to discriminate which shapes fell at either the local or the global level. When participants had to discriminate between self and stranger shapes, there was interference from self distractors on responses to stranger shapes, and this held both when the target was at a local level and when it was at a global level. In contrast, there was no differential interference from friend distractors on stranger targets (or vice versa). The pattern of the results for the self versus stranger discrimination mimics that previously reported when the perceptual saliency of the stimuli was varied by either blurring the hierarchical shapes (making the global shape more salient) or by using high-contrast local shapes that alternated in color (making the local shapes more salient). With such stimuli there is differential

interference from a more salient distractor on a less salient target (e.g., greater interference from the global shape on responding to a local item when the shape is blurred, and greater interference from the local shape on responding to the global shape when high-contrast letters are used; see Mevorach, Humphreys, & Shalev, 2006). The similarity of these behavioral effects suggests an analogy in which having a self-associated shape at a global level is akin to blurring the hierarchical stimulus while having a self-associated shape at a local level is asking to increase the contrast of each local stimulus.

The behavioral results from Sui, Liu, et al. (2013) were matched too by fMRI data. When participants have to respond to a target that is low in perceptual saliency and ignore a high-saliency distractor, there is increased activity in part of the attentional control network—the left intra-parietal sulcus (IPS)—consistent with this brain region being recruited to suppress the salient distraction (Mevorach, Hodson, Allen, Shalev, & Humphreys, 2010). Likewise, there was recruitment within the left IPS when participants had to select a low-saliency stranger shape and ignore a higher saliency self-related shape. The increased activation associated with rejecting the high-saliency self overlapped with the increase found when participants reject a distractor with high perceptual saliency (see Figure 2; Sui et al., 2012). These data indicate that self-association acts similarly to

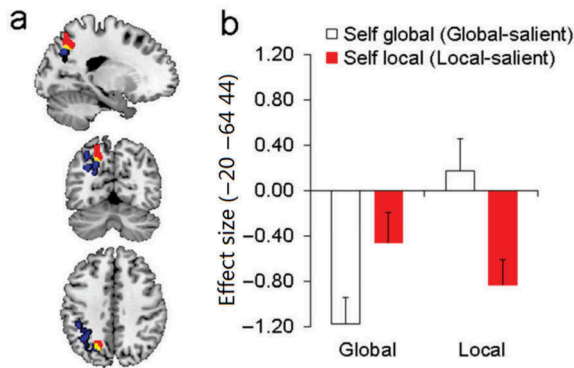


Figure 2. Brain activity when participants ignore salient distractors vs. when targets are salient, in hierarchical figures. (a) Activity in the left IPS corresponding to (1) the contrast between self as distractor vs. self as target (red), (2) the contrast between distractors with high perceptual saliency and targets with high perceptual saliency (blue), and (3) a common region of activation when distractors are either the self or stimuli with high perceptual saliency (yellow). (b) Beta weights within the left IPS region common to the self and perceptual saliency as a function of the level and nature of the target (local or global, self or stranger). Note that the beta weights show a cross-over interaction. When responding to a global target, there is greater activation when the self-related stimulus is a local distractor compared with when the self-related shape is the target. When responding to a local target, there is greater activation when the self-related stimulus is a global distractor compared with when it is the target (from Sui, Liu, et al., 2013).

alterations in the perceptual saliency of a stimulus, both in terms of behavior and in terms of the linked brain activity. We can say that self-association alters the social saliency of stimuli. Moreover, the attentional control network interacts with the social saliency network to determine performance.

A framework for the interaction between the self and attention: The Self-Attention Network (SAN)

To account for the above results, we propose a new framework for the interaction between the self and attention which we term the Self-Attention Network (SAN). This framework is presented in Figure 3. The network has three main processing nodes: (1) a general-purpose top-down attentional control network (here we highlight two areas implicated in our work—the dorso-lateral prefrontal cortex, DLPFC, and the intra-parietal sulcus (IPS)); (2) a self-representation housed in the ventro-medial prefrontal cortex (vmPFC); and (3) a region involved in bottom-up orienting (the posterior superior temporal sulcus, pSTS). We argue that interactions between these processing nodes determine our response to stimuli linked to the self rather than other people.

We propose that self-driven attention orienting is modulated by excitatory connectivity between the vmPFC and the pSTS (black arrow). Evidence for this connectivity is presented in Figures 3b (left) and 3c. Figure 3b (left) illustrates the positive correlation across participants for neural activity in the vmPFC and left pSTS (LpSTS) when matching responses are made to self-related stimuli (data from Sui, Rotshtein, et al., 2013). Figure 3c shows the best fitting model of the brain activity, generated using dynamic causal modeling, in which strong excitatory connections are proposed from vmPFC to the LpSTS. The vmPFC is rapidly triggered by the presence of self-related stimuli—an idea similar to that proposed by Bar and colleagues in relation to fast triggering of object-related memories in orbito-frontal cortex, which modulates subsequent visual processing (Bar et al., 2006). We argue that this rapid activation of the vmPFC in turn activates the pSTS node so that it is primed to respond to self-related items, generating a self-bias effect in perception and attention.

In addition, the framework highlights that the top-down attentional control network can moderate bottom-up driven self-related activity in the vmPFC and pSTS. For example, under perceptual matching conditions, fast triggering of a response to a self-related stimulus could generate an error on a

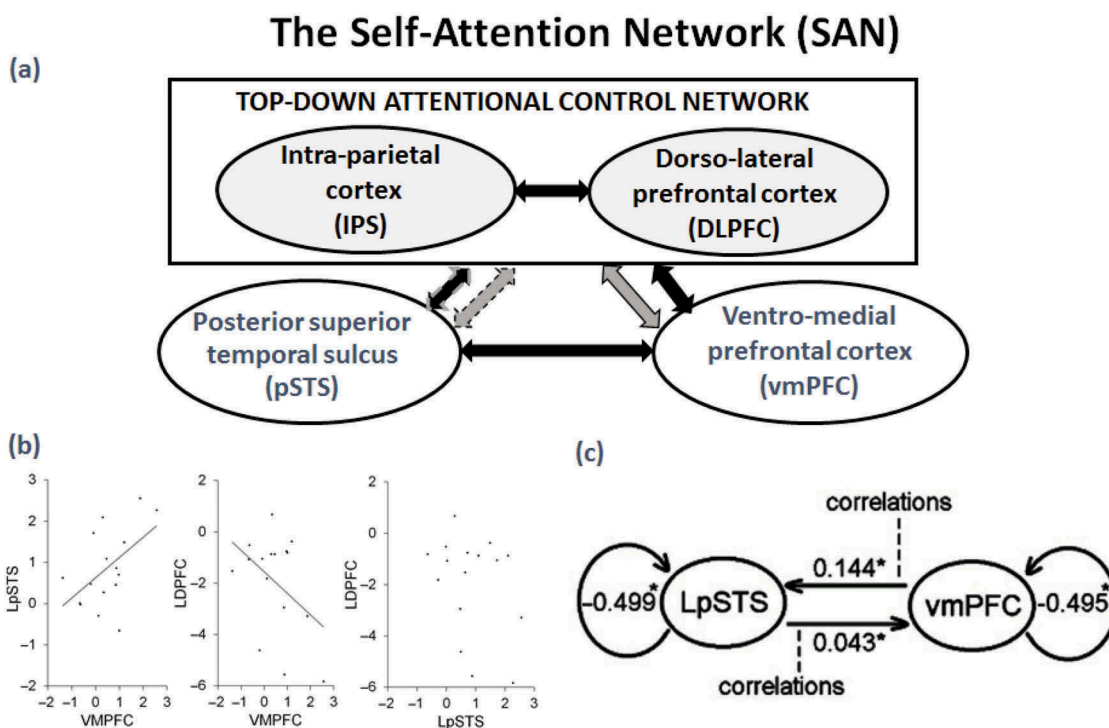


Figure 3. (a) The Self-Attention Network (SAN). Here we distinguish between a top-down attentional network (including the intra-parietal sulcus (IPS) and the dorso-lateral prefrontal cortex (DLPFC)) and a network that responds in a bottom-up fashion to self-related information (the posterior superior temporal sulcus (pSTS) and the ventromedial prefrontal cortex (vmPFC)). Black arrows indicate excitatory connections. Grey arrows indicate inhibitory connections. Dotted arrows (to and from the pSTS) highlight that there is currently little direct evidence for these functional connections. (b) Correlations of brain activity in the left pSTS (LpSTS) and vmPFC (left panel), in the left DLPFC and the vmPFC (middle panel), and the left DLPFC and left pSTS (right panel) when matching self-related stimuli (data from Sui, Rotshtein, et al., 2013). (c) The best fitting dynamic causal model of brain activity in perceptual matching of self-related stimuli (from Sui, Rotshtein, et al., 2013).

mismatching trial when a self-related stimulus is paired with a stimulus associated with another person. To mitigate against this, there may be top-down inhibition of self-representations from the attentional control network (grey arrow). Data consistent with this are shown in Figure 3b (middle panel), which indicate a negative correlation between neural activity in the DLPFC and the vmPFC under perceptual matching conditions (data from Sui, Rotshtein, et al., 2013). Our results on rejecting self-distractors in hierarchical stimuli (Sui, Liu, et al., 2013) also implicate the IPS in inhibitory suppression of self-stimuli, though the locus of inhibition from the IPS to the vmPFC (for example) has yet to be established. On the other hand, there are many circumstances in which it can be beneficial to allocate attention to self-representations—for example, to enhance encoding in memory (Conway, 2005). In our own work we have noted that participants can adopt positive expectancies for self-related stimuli (e.g., in perceptual matching, when self-related items have a high frequency of occurrence), which then dominate performance relative to expectancies held

for other people (Sui et al., 2014). Thus, in addition to positing inhibitory connections, we also propose that excitatory connections from the attentional control network can modulate activity in the vmPFC (black arrow), and that this excitatory loop generates attentional enhancement for the self.

Evidence for connectivity between the attentional control network and the pSTS is more sparse. For example, Figure 3b (right graph) shows no evidence for a correlation between neural activity in the DLPFC and the pSTS under conditions of perceptual matching (data from Sui, Rotshtein, et al., 2013). Also, it is not clear that attentional suppression of self-related distractors mediated by the IPS (Sui, Liu, et al., 2013) operates through the pSTS. Mevorach et al. (2010) examined the neural locus of the suppression of salient distractors in hierarchical figures and found evidence for the suppression of early visual areas, which would subsequently decrease bottom-up activity in the pSTS; however, there was no evidence for direct suppression of the pSTS. Another possibility is that the attentional control network determines

directly the spatial region that pSTS activity is sensitive to, and in this way governs whether self-related stimuli are activated in a bottom-up manner or not (cf. Keyes & Dlugokencka, 2014). Direct attentional modulation of pSTS activity would explain why damage to the pSTS can lead to increased attentional biases (Sui et al., *in press*), if there is then reduced top-down attentional control. Clearly though, further work is required to establish the functional connectivity between the attentional control network and the pSTS that may modulate bottom-up orienting to the self.

BEYOND THE SELF

One interesting aspect of self-biases is that they can vary across individuals and, even in simple perceptual matching tasks, the magnitude of the bias is a robust marker of individual differences across time (Humphreys & Sui, *in press*). There is evidence that one factor generating individual differences in self-bias is the culture that individuals have experienced. In particular, participants from Western cultures tend to show stronger self-biases (e.g., in face orientation judgements; Sui, Liu, & Han, 2009) than individuals from Asian cultures, perhaps reflecting greater individualism in Western participants and collectivist processing in Eastern cultures. Interestingly, these cultural differences are apparent within the early N2 component which is modulated by self-face information, suggesting cultural effects on attention.

As well as showing biases toward stimuli relating to ourselves, there is much work showing biases extend to the groups that we categorize ourselves as being members of. Being a member of a group is commonly accompanied by categorizing the “self” and the “others” into in- and out-groups (Amodio, 2009; Tajfel, 1982) and this affects how strongly people empathize with others when they watch simple actions (Mathur, Harada, Lipke, & Chiao, 2010; Molenberghs, Halász, Mattingley, Vanman, & Cunnington, 2013). There are also effects on putatively perceptual tasks. For example, in the well-known “own race effect,” individuals show enhanced memory for faces belonging to their own racial group relative to faces belonging to other races (e.g., Brigham, Bennett, Meissner, & Mitchell, 2007). The enhanced performance can be linked to the greater processing of the configural properties of own race faces (e.g., based on the spatial relations between different facial features) (Michel, Corneille, & Rossion, 2007, 2010). The magnitude of this effect can vary with our experience with faces from other

races with the own-race bias reducing as experience increases with other race faces (Brigham & Malpass, 1985). However, there is also evidence that biases can be rapidly established based on in- and out-group coding. For example, there is greater configural coding if other race faces are categorized as belonging to the observer’s own university group (Cassidy, Quinn, & Humphreys, 2011; Hugenberg & Sacco, 2008). These data suggest that perception can undergo rapid modulation depending on whether participants are motivated to classify individuals as in- or out-group members.

Moradi, Sui, Hewstone, and Humphreys (*in press*) used the shape association procedure of Sui et al. (2012) to evaluate if group-level biases could modulate perceptual matching performance. They had football supporters form associations between (1) their favorite team, their rival team, and a neutral team and (2) three geometric shapes. The task was then to judge whether correct shape-team pairs were presented or whether the stimuli had been re-paired. As in the studies of self-bias, there was an advantage for stimuli associated with the participants’ in-group over stimuli associated with neutral or with rival teams.

Moradi, Duta, Hewstone, and Humphreys (*sub.*) extended this by employing group-associated stimuli in pro- and antisaccade tasks—where participants either had to look toward or look away from a target. They found that participants made more directional errors on prosaccade tasks (looking away from the target) when stimuli associated with the rival team were presented. The converse of this was that participants made more directional errors on antisaccade tasks (looking toward the target) for stimuli associated with the in-group team. These data on pro- and antisaccade tasks indicate that it was difficult for participants to resist attending to an in-group association and to direct attention to an out-group, rival association. The results suggest that the biased responses to our preferred stimuli can be extended from the self to the group level, and they reflect attentional biases to salient in-group stimuli.

One other way in which social context can extend attentional biases beyond the self comes from studies of joint action. In many everyday circumstances we co-operate with other people in performing a task (e.g., when two people carry a piece of furniture together), and in these circumstances it may behoove us to attend not only to stimuli related to ourselves but also those relating to the person we are engaged in the joint action with. This has been examined in studies focusing on the relations between working memory and attention. There is

considerable evidence that there can be effects on attention from stimuli being concurrently held in working memory (WM; see Soto, Hodson, Rotshtein, & Humphreys, 2008, for a review). For example, Soto, Heinke, Humphreys, and Blanco (2005) had participants hold a shape in WM while they performed a search for a different target (an oriented line). The search display could contain shapes as well as lines, and the shapes could be the item being held in WM or a new item. Maintenance of the WM item was tested after the search display. When the WM item re-appeared in the search display alongside the target line (on a valid trial), search was facilitated relative to when the WM item re-appeared alongside a distractor line (on an invalid trial). He, Lever, and Humphreys (2011) examined this WM-guidance effect under conditions of joint action. In this case, the task was performed by two participants and they were cued as to who was to carry out the search task on a trial. Prior to the trial one of three categories of stimulus was presented. One category constituted the WM items for one participant (participant 1; e.g., furniture); one category constituted the WM items for the second participant (participant 2; e.g., vehicles); one category was irrelevant and did not have to be maintained in WM by either participant. He et al. assessed whether only the self-related WM item directed attention (e.g., furniture, for participant 1) or whether, under the condition of being jointly engaged in the task, attention might also be directed to the WM stimulus that was relevant to the co-actor (e.g., if a vehicle appeared in the search display for participant 1). While the strongest effects on attention stemmed from the re-appearance of the self-related WM item in the search display, there were nevertheless effects based on the co-actor's memory item (importantly, there were minimal effects of the third category, which neither participants had to maintain). This indicates that, when people engage in joint action, their attention systems are modulated not only by self-related information but also by information relevant to their partner in the task. In addition, like self-bias effects on face processing (Sui et al., 2009), the degree to which participants attend to information relevant to their co-actor rather than themselves is modulated by variations in individualism and collectivism across cultures (He, Sebanz, Sui, & Humphreys, 2014). Again, the effects of self-bias on attention are infiltrated by culture.

These effects of joint action are also dependent on participants having sufficient resources available to maintain attention to the other person (and perhaps to suppress responses to the self). Humphreys and Bedford (2011) tested joint action effects in patients with lesions to the frontal lobes and impairments in

executive attentional control. The patients were instructed to pay attention to their co-actor at the start of the experiment. Humphreys and Bedford found that the frontal patients initially showed effects of joint action (their performance was modulated by the presence of the other person), but, unlike controls, the joint action effect decreased across trial blocks. These results suggest that, due to their reduced executive control, the frontal patients were less able to maintain attention to the other person, and so showed weaker effects of joint action across the trial blocks.

Exactly how these cultural, group, and co-actor effects influence the neural networks determining attentional control over perception and action has yet to be established. There are proposals that effects of in-group identification on cognition are built upon self-related responses—with the in-group becoming linked to the representation of the self (the idea of “identity fusion,” see Swann, Jetten, Gómez, Whitehouse, & Bastian, 2012). In this case, we may expect an overlap between the functional and neural responses associated to the self and the in-group. In contrast, the effects of culture and joint action may reflect the degree of top-down attentional control that may exist in responding to self-related stimuli, which may be highly context-dependent and increased in East Asian cultures, and when we engage with a co-actor in a task. Long-term cultural effects may also reflect weaker self-representations themselves—though evidence that strong self-related responses can be established in East Asian participants under appropriate priming conditions (Sui, Hong, Liu, Humphreys, & Han, 2013) indicates that the effects may be quite malleable.

SUMMARY

We have presented evidence on the inter-relations between attention and self-relevant stimuli. On the one hand we have argued that self-relevant stimuli are powerful cues for attention, they can modulate performance in a relatively automatic manner, even sometimes without awareness. The data further suggest that self-related stimuli change their salience for attentional selection (there are effects of social as well as perceptual saliency on selection). These effects can also extend beyond the self to include stimuli associated to a participant's in-group and stimuli that are relevant to their co-actor when individuals participate in joint action. On the other hand, we have reviewed evidence that self-biases can be affected by attention and that self-bias modulates

top-down attentional processing. To account for the results, we propose a Self-Attention Network (SAN) in which nodes that respond to self-related stimuli (the vmPFC and pSTS) interact with nodes within an attentional control network to determine perception and action.

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Commentaries

How does the ‘rest-self overlap’ mediate the qualitative and automatic features of self-reference?

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Abstract: The target article points out the qualitative and automatic features of self-reference while leaving open the underlying neural mechanisms. Based on empirical evidence about rest-self overlap and rest-stimulus interaction being special for self-related stimuli, I postulate that the resting state shows self-specific organization. The resting state’s self-specific organization may be encoded by activity balances between different networks which in turn predispose the qualitative features of subsequent self-related stimulus-induced activity in, for instance, SAN as well as the automatic features of self-reference effects.

Humphrey and Sui (2015) point out two central features of the self-reference effects, its qualitative and automatic features. There is qualitative difference between self and non-self: There is a continuum of effects from familiar to non-familiar persons while there is no continuum between self-related and familiar stimuli in psychological processing. Moreover, they emphasize

the pre-attentive features of self-reference effects entailing their automatic features.

What are the neural mechanisms underlying the apparently qualitative and automatic features of the self-reference effect? Without explicitly referring to these two features in the later part of the paper, they assume the self-attention network (SAN) to be central for that which consists of three nodes, VMPFC, DLPFC and IPS, and pSTS.

How now must neural activity be like in order to allow for the qualitative and automatic features of the self-reference effect as mediated by SAN? Empirical data show substantial neural overlap between the levels of resting state activity and self-related stimulus-induced activity in, especially, the cortical midline structures (CMS) as core of the default-mode network (DMN). Using H2O PET, D’Argembeau et al. (2005) early reported no activity change in VMPFC during self-related stimuli when compared to resting state activity levels in the same regions. Schneider et al. (2008) observed that preceding self-related stimuli modulated subsequent resting state activity (i.e., intertrial intervals) to a much higher degree than non-self-related activity. Whitfield-Gabrieli et al. (2011) reported self-related activity in the same regions of CMS that also showed high degrees of resting state functional connectivity. Qin and Northoff (2011) conducted a meta-analysis of both resting state and self-reference studies and showed substantial neural overlap between both, amounting to what I call the ‘rest-self overlap’.

What exactly is meant by ‘rest-self overlap’? The rest-self overlap only describes regional overlap but does by itself not imply anything about the relationship between resting state activity and self-related stimulus-induced activity, i.e., rest-stimulus interaction (Northoff, Qin, & Nakao, 2010). Going beyond mere rest-self overlap, one requires a special form of rest-stimulus interaction between resting state and self-related stimuli to account for the qualitative and automatic features of self-reference.

Qin et al. (2013) investigated the impact of two different resting state activity levels in auditory cortex, eyes closed (low levels) and open (higher levels), on own, familiar, and stranger names. Presupposing a purely additive model of

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rest-stimulus interaction, one would expect that higher levels of auditory cortical resting state activity as during eyes open lead to higher levels of stimulus-induced activity. This was indeed the case for both familiar and stranger names.

This pattern was not observed for the own name, however. The own name already elicited high levels of stimulus-induced activity during the low level of resting state activity, i.e., eyes closed, which was as high as the one during the high level of resting state activity, i.e., eyes open. This suggests non-additive interaction between resting state and self-related stimuli that is qualitatively different from the additive interaction of familiar and stranger names.

Does the resting state impact the degree to which self-reference is attributed to a stimulus? Bai et al. (2015) observed in an EEG study that the level of pre-stimulus alpha power (i.e., -600 to 400 ms) predicted the degree of self-reference (i.e., high or low) subjects attributed to subsequent emotional and neutral stimuli. Moreover, the degree of pre-stimulus alpha power was predicted by the resting state concentration of Glutamate in VMPFC. These data show the resting state level, i.e., pre-stimulus alpha power and Glutamate, to impact stimulus-induced activity including the degree to which stimuli are perceived as self-related.

Taken together with other data, these data suggest the resting state activity to exert significant impact on subsequent stimulus-induced activity and its perception as self-related. Though central, such special rest-stimulus interaction does not seem to be limited to the CMS as part of DMN but may rather concern their balance to other networks like CEN (with DLPFC and IPL) and sensorimotor networks (see, Nakao, Bai, Nashiwa, & Northoff, 2013; Nakao, Ohira, & Northoff, 2012; Vanhaudenhuyse et al., 2011). The activity balance between different networks may encode a certain degree of self-specificity in the resting state that therefore exhibits self-specific organization (Northoff, 2014a, 2014b).

Depending on its lower or higher degrees of encoded self-specific organization, the resting state may then react differently to subsequent stimuli: The resting state may for instance react qualitatively different to those stimuli, e.g., self-related, that it already knows due to its own encoded self-specific organization (higher resting state's self-specific organization should lead to higher degrees of qualitative self-reference). Hence, one predicts the following: Higher degrees in the resting state's self-specific organization, i.e., the balances between different networks, may lead

to higher degrees of self-specificity attributed to external stimuli and higher automatic self-reference effects as mediated by the stimulus-induced neural balances within SAN as so well described by Humphrey and Sui (2015).

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The self-relevance system?

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Abstract: We suggest that the Self Attention Network (SAN) maybe part of a larger self-regulatory system, which we term the *Self-Relevance System* (SRS) of which the “core” or default network is a major part. It is within the core network that memories are generated and the future imagined. Such memories and imaginings are the basis of preoccupations. Within the SRS then preoccupations drive the emergence of attentional biases (ABs). ABs in turn are modulated by the SAN activating and inhibiting circuits that shape behavior. We consider briefly how this might function in dysfunctional appetitive behaviors, e.g., substance abuse.

It has long been known that the self plays a central role in many forms of cognition, from attention and perception to memory and emotion. Indeed, it may be critical in giving rise to memories that can later trigger recollective experience (Conway & Dewhurst, 1995). The link between self-relevance and attention has also been demonstrated in previous studies. For example, the relationship between automatic and controlled

attentional processing in self-referential encoding tasks can be seen in the studies reported by Turk et al. (2011). They used a temporary ownership task in which items were assigned to self or other on the basis of a color cue. Responses to self-relevant cues were associated with a narrowing of spatial attention (occipital P1 component) to the location of the owned object. This early, automatic response to the detection of self-relevance was followed by a later increase in the P300 component associated with higher-order, top-down modulation of attention and executive processing. Indeed, Turk, van Bussel, Waiter, and Macrae (2011) proposed a temporal model in which activity in attentional and reward circuits in frontal cortex associated with object ownership was followed by activity in lateral posterior regions associated with attention for action. Interestingly, activity in this network was suppressed during the processing of items belonging to others.

The main contribution of Humphreys and Sui ([this issue](#)) is in identifying a potential self-attention network (SAN) in the temporal lobes and ventromedial prefrontal cortex that is modulated by an inhibitory network in intra-parietal sulcus and dorsolateral prefrontal cortex. It seems to us that the inhibitory control is essential as not all events are high in self-relevance and those that are may attenuate other processes, for example, the encoding of memory details. It is interesting that experiences of intense self-relevance, such as trauma, often lead to memories low in detail with amnesic gaps (Conway, Meares, & Standart, 2004). Thus, controlling attentional biases (ABs) created by high self-relevance is perhaps critical to optimum cognitive functioning.

The SAN, however, may be part of a larger and more complicated *self-relevance system* (SRS) encompassing a wide range of cortical networks collectively known as the *core* or *default* network (Buckner, Andrews-Hanna, & Schacter, 2008).

When attention is unfocussed, the core system is characterized by activation in anterior and posterior networks, the same networks that become active during remembering and imagining (Conway & Loveday, 2015). But when attention is unfocussed, remembering and imagining are probably the main activities of the cognitive system and their outputs are the representations that the SAN attends to. Inhibiting or facilitating such outputs shapes ABs and behavior.

In this regard an interesting and important role for the SAN may lie in generating ABs in, for instance, appetitive behaviors both functional and dysfunction, e.g., substance abuse. Alcohol abuse can lead to an AB for alcohol-related information (Cox, Fadardi, & Pothos, 2006), just as hunger is associated with ABs

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for food-related information (Tapper, Pothos, & Lawrence, 2010). Preoccupation may explain how SAN ABs arise, i.e., an alcohol abuser is preoccupied with consuming alcohol and so alcohol-related information becomes salient (Klinger & Cox, 2011). Could self-biases arise analogously? Plausibly, we are preoccupied with ourselves, what we own, or perhaps by how others perceive us. Additionally, some key characteristics of decision-making, such as loss aversion, make sense only in relation to the self. Perhaps self-preoccupation in the SRS could result in an AB for the self, overall.

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The function of the self-attention network

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Abstract: This commentary links Humphrey and Sui's proposed Self-attention Network (SAN) to the memory advantage associated with self-relevant information (i.e., the self-reference effect). Articulating this link elucidates the functional quality of the SAN in ensuring that information of potential importance to self is not lost. This adaptive system for self-processing mirrors the cognitive response to threat stimuli, which also elicit attentional biases and produce characteristically enhanced, episodic representations in memory. Understanding the link between the SAN and memory is key to comprehending more broadly the operation of the self in cognition.

Our understanding of the cognitive systems triggered by perception of self-relevant cues has grown significantly in the past 10 years, as Humphreys and Sui's timely target article makes clear. Their proposed "Self-Attention Network" (SAN) is built on a solid foundation of recent behavioral and neural research on self-attention biases, which reveals a combination of top-down and bottom-up processes involving both the attention control network and areas associated with self-referential cognition. While the SAN framework is a valuable step forward in refining our understanding of self-processing biases, one important consideration that is not addressed in the target article is the *function* the SAN, an aspect that should be central to any big-picture conceptualization of self-processing biases.

I submit that the SAN functions to ensure that information of potential relevance to self is preferentially encoded; in other words, attention biases serve to support the self-reference effect in memory (Symons & Johnson, 1997). This robust memory advantage for information associated with self at encoding is elicited by even minimal self-stimulus connections, such as simultaneous presentation of stimuli with a self-cue, or temporary ownership in a sorting game (Cunningham, Turk, Macdonald, & Macrae, 2008; Turk, Cunningham, & Macrae, 2008). It serves the important ecological function of ensuring

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that information of potential use to self is not lost (Cunningham, Brady-Van den Bos, Gill, & Turk, 2013).

This functional explanation of the SAN mirrors other attention-based memory effects, such as the cognitive response to threat stimuli. When a threatening cue is perceived, it captures attention even when the cue is not task-relevant, because survival is a constant underlying goal (Öhman & Mineka, 2001). Increases in attentional focus and neurotransmitter levels in response to threat cues result in memories that are characterized by binding and episodic recollection (see Hadley & MacKay, 2006). The effects of self on cognition strikingly echo this system: self-relevance is perpetually goal-relevant, self-cues attract attention via the SAN, and resultant memories are characteristically episodic in nature, bound with information from the encoding context (Conway & Dewhurst, 1995).

Supporting the idea that the self improves episodic binding in a manner akin to emotional processing, we have shown that while centrally presented self-cues (e.g., own-name, own face) attract attention, they do not detract from the processing of simultaneously presented peripheral stimuli as might be expected; rather, these are remembered better than stimuli presented with cues of other-referents (Turk et al., 2008). Interestingly, recent data (Cunningham & Allan, 2015) suggests that when stimuli are presented with self- and other-faces at short SOAs (< 250 ms), the usual memory advantage for those presented with self over other does not emerge. However, when the SOA is longer (700 ms), memory for other-referent stimuli decreases significantly while self-referent stimuli remain well-remembered, creating a self-reference effect. This suggests that the self continues to bind the stimuli and cue together when the binding produced by temporal proximity has lapsed.

Extending Humphreys and Sui's argument, information relevant to self is subject to biases that combine to produce a robust and adaptive memory advantage. Understanding the link between the SAN and memory is key to comprehending more broadly the operation of the self in cognition.

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Evaluating automatic attentional capture by self-relevant information

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Abstract: Our everyday decisions and memories are inadvertently influenced by self-relevant information. For example, we are faster and more accurate at making perceptual judgments about stimuli associated with ourselves, such as our own face or name, as compared with familiar non-self-relevant stimuli. Humphreys and Sui propose a “self-attention network” to account for these effects, wherein self-relevant stimuli automatically capture our attention and subsequently enhance the perceptual processing of self-relevant information. We propose that the masked priming paradigm and continuous flash suppression represent two ways to experimentally examine these controversial claims.

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According to Humphreys and Sui's self-attention network (SAN), incoming sensory information related to the "self" rapidly activates self-representations housed within the ventromedial prefrontal cortex (vmPFC). Excitatory connectivity between the vmPFC and regions involved in bottom-up visual orienting (i.e., the posterior superior temporal sulcus) subsequently prime the processing of self-relevant items. Yet whether self-relevance is computed pre-attentively remains an open question. We propose that the masked priming paradigm can be used to index the automaticity of self-biases in perceptual processing by revealing whether self-relevance can be computed in the absence of conscious awareness and, crucially, independently from spatial attention. In a typical experiment, a "prime" stimulus is presented very briefly and heavily masked such that it cannot be consciously perceived. The task is to categorize a subsequent visible target as, for example, a "person" or "animal", by making a left/right button-press response. When the prime and target are congruent (e.g., person prime followed by person target), response times to the target are faster than when the prime and target are incongruent (e.g., animal prime followed by person target; Finkbeiner & Friedman, 2011).

Critically, by cueing attention toward or away from a prime's location in space, one can determine whether this type of stimulus can engage cognitive processes both when attended and when unattended (see Finkbeiner & Palermo, 2009). Therefore, if self-relevant stimuli automatically activate self-representations and attract attention, one would expect a non-conscious, self-relevant prime to produce priming even when attentional resources are engaged elsewhere. This finding would satisfy the first claim of the SAN: A fast, *automatic* deployment of attention toward self-relevant stimuli.

Neuronal firing rates for attended stimuli become magnified, particularly when these cells encode higher-level cognitive representations (Maunsell, 2004). One could assume, therefore, that the aforementioned increase in attention will result in increased firing rates amongst cells responding to self-relevant information. We will make this tentative assumption when considering Humphreys and Sui's second claim: That of enhanced processing of self-relevant stimuli.

In continuous flash suppression (CFS; Tsuchiya & Koch, 2005), distinct colorful patterns ("Mondrians") are flashed successively into one eye, delaying awareness for a lower contrast and stationary image presented to the other eye. When the contrast of the image shown to the "suppressed" eye is gradually increased, the time taken for it to reach

consciousness can vary according to high-level stimulus dimensions. If an image is easier to make sense of/assemble because of bottom-up familiarity (as might be the case for an upright versus an inverted face), one should expect a benefit in recognition time for that image (e.g., Jiang, Costello, & He, 2007). However, should an experimental image (e.g., one's own face) capture attention and receive more neural processing relative to an equally-familiar upright control image (e.g., a stranger's face), recognition speed for the experimental image should be slower. This "deficit" in recognition speed has been previously observed with negative valence words shown in CFS, and is believed to reflect the greater habituation (i.e., a cognitive aftereffect) that accrues for stimuli that receive additional neural processing (Huber, 2015; Prioli & Kahan, 2015).

Behavioral evidence in support of the SAN is inconclusive. The methodological approaches outlined above will provide convincing evidence in support of two important claims emerging from the SAN model: (1) self-relevant stimuli automatically attract visual attention and (2) perceptual processing of self-relevant stimuli is enhanced.

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Connectivity between ventromedial prefrontal cortex and posterior superior temporal sulcus

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Abstract: The well-articulated Self Attention Network (SAN) framework accounts for a great portion of the available evidence on neurocognitive interactions between self-bias phenomena and attention. I argue that more work is necessary to refine our understanding about the effective and functional connectivity of the different nodes of the proposed network. In particular, the nature of the control of ventro-medial prefrontal cortex over posterior superior temporal sulcus has to be worked out further. Simple excitatory connections between these two nodes, as proposed by the SAN model, do not satisfactorily account for existing neuropsychological dissociations and are not fully warranted by neuroimaging evidence.

Humphreys and Sui propose a self-attention network (SAN) framework, which describes complex interactions between a fronto-temporal network specifically dedicated to self-attention and the fronto-parietal attentional network. The model explains well most of the existing multimodal data on self-bias and its interactions with attentional processes, including experimental psychology, functional Magnetic Resonance Imaging (fMRI) and neuropsychological evidence.

My concerns about the SAN model regard the hypothesis of strong and mostly unidirectional excitatory connections from the ventro-medial prefrontal cortex (vmPFC) to the posterior superior temporal sulcus (pSTS). This hypothesis is mainly based on positive correlations between fMRI activations in these two regions and on dynamic causal model results.

First, it seems unlikely that the connectivity between these two regions is completely excitatory. This would not fit with available neuropsychological evidence (Sui, Enock, Ralph, & Humphreys, 2015).

These lesion data show that damage to pSTS increases self-bias effects, while damage to vmPFC decreases them. Excitatory connectivity between the vmPFC, which is clearly related to self-bias (e.g., Jenkins & Mitchell, 2011), and a target region such as the pSTS which, as Humphreys and Sui argue, has a role in attending self-related stimuli, should enhance the self-bias, when the network is fully working. On the contrary, damage to either one of these regions should decrease the self-bias, which is the opposite of what was observed with pSTS lesions. A possible solution would be, for instance, to suppose a modulatory role of pSTS through inhibitory feedback connections toward the vmPFC.

Moreover, one should be careful in interpreting the direction of a positive correlation between fMRI activations in two regions as a univocal marker of excitation versus inhibition. Not only when a source region sends excitatory signals to another target region, but also inhibitory ones, metabolic demands in the latter region may increase and the fMRI activation pattern of the two regions may appear as positively correlated. In the neocortex of animal models, increased glucose consumption is associated with inhibition of auditory (Nudo & Masterton, 1986) and somatosensory (McCasland & Hibbard, 1997) neurons. In the latter study, glucose metabolism was even stronger in inhibitory (GABAergic) neurons than in excitatory (glutamatergic) ones. Unfortunately, none of these studies directly measured oxygen consumption, which is more directly related to fMRI than glucose metabolism. More generally, however, given that excitatory and inhibitory neurons provide complex and interacting contributions to brain function, it is difficult to unequivocally interpret which of them causes metabolic changes based on fMRI results (Buzsáki, Kaila, & Raichle, 2007).

Thus, the alternative interpretation that these two fronto-temporal nodes are linked, directly or indirectly, also through inhibitory connections not predicted by the putative SAN model cannot be disregarded so easily. The presence of inhibitory connections would explain the behavioral dissociation between lesions in vmPFC and pSTS without being necessarily incompatible with the presence of positive correlations in fMRI activations, although I must admit that this scenario would not fully fit existing dynamic causal model results.

Finally, it is implausible that, from the structural point of view, the effective connectivity between these two regions is direct, in the sense that there are white matter tracts connecting them without intervening nodes. Tracer studies in animal models show that the vmPFC has mainly short-range, local

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cortico-cortical projections to and from other prefrontal regions as well as to the sensory-motor cortices and the limbic system (Cavada, Compañy, Tejedor, Cruz-Rizzolo, & Reinoso-Suárez, 2000), a pattern largely confirmed with non-invasive Diffusion Tensor Imaging data in humans (Lehéricy et al., 2004).

In conclusion, future work should not only attempt to better characterize the effective and functional connectivity between vmPFC and pSTS, but also try to elucidate which intermediate cortical or subcortical nodes are missing in the SAN model and what modulatory role they may play.

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Top-down control and directed attention in self-reference effects: Goal-directed movements and the SAN

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Abstract: We focus on Humphreys and Sui's postulations that self-reference effects are not necessarily pre-attentive, and the self and top-down attention interact in the SAN. If so, top-down factors (goal-relevance, directed attention) should interact with self-reference effects. Our pilot data from unspeeded reach-to-grasp actions show differences in trajectories when reaching toward self- or other-relevant objects. We speculate that goal-directed actions are suited to studying the top-down control in self-reference effects. Because goal-directed action paradigms allow broad scope for modulating attention and top-down control, they will be useful for disambiguating the roles of directed attention, inhibition, and (social) context.

This timely review of emerging literature covers behavioral studies and probable neural substrates underpinning the Self Attention Network (SAN). Clearly, the self-other boundary serves as an organizing principle for cognitive processes such as recall, recognition, and attention. The authors make two inter-related postulations that will be crucial for investigations of the SAN: That self-reference effects (SREs) in behavior are not necessarily “pre-attentive,” and that the SAN interacts with top-down control to direct behavior.

If SREs are not pre-attentive, top-down factors should modulate performance. Humphreys and Sui review evidence that when self-associated stimuli are goal-relevant and within the focus of spatial attention, their processing is enhanced. Further, self-associated stimuli benefit more from increased expectancy than other-associated stimuli, yet do not suffer when their probability of occurrence decreases (Sui, Sun, Peng, & Humphreys, 2014). This suggests that processing of goal-relevant self-associated stimuli can be enhanced effectively, but not suppressed, when they are goal-relevant.

We think that the SREs will be evident also in goal-directed actions such as reach-to-grasp. Using goal-directed actions we can measure execution parameters as well as RTs, which may disambiguate mechanisms of attention and inhibition in SREs.

In a pilot study, 24 female participants (aged 18–36, $M = 21.25$) who gave informed consent sat at a table and reached with the right hand and picked up a card positioned 32 cm from their hand. Each card depicted

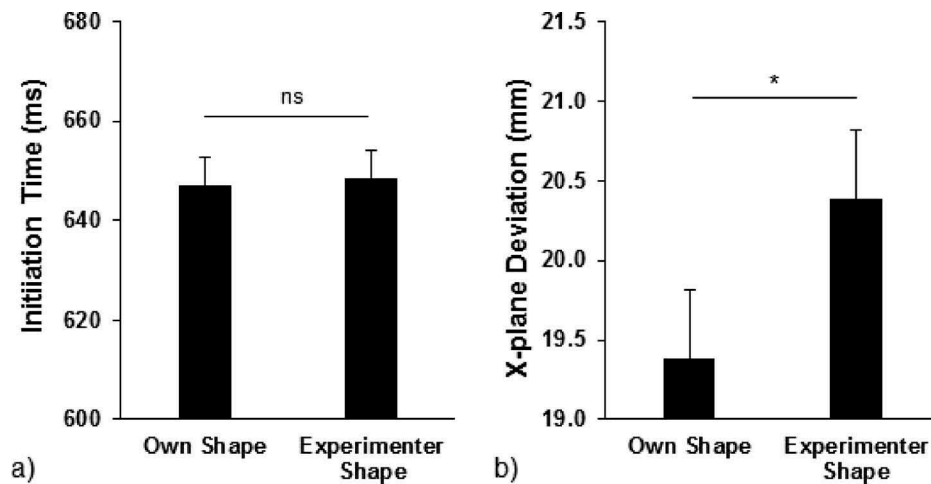


Figure 1. Mean initiation time (a) and X-plane deviation (b) toward self- and experimenter-shape cards (errors depict one standard error of the mean).

one of two shapes (oval or rectangle). Participants were told that one shape “belonged” to them while the other “belonged” to the experimenter. Participants closed their eyes while cards were placed, opened them to a sound cue, and initiated unspeeded reaches. They grasped the card at the top right corner, and placed it in one of two cardholders (“self” or “experimenter”) near the start position. Qualisys Oqus motion-capture cameras recorded motion of reflective markers on participants’ wrists.

For each reach we calculated initiation time and rightward deviation in the x plane, that is, maximum displacement (mm) from the hypothetical straight line from the wrist marker’s initial location to the grip location. Participants’ initiation times to own-shape and experimenter’s-shape cards did not differ ($t(23) = 0.38$, $p = .706$; Figure 1, panel a). Reaches to own-shape cards followed a more direct trajectory than those toward experimenter’s-shape cards, as shown by lower x-plane deviation ($t(23) = 2.139$, $p = .043$; Figure 1, panel b).

Note that we required a particular goal-directed action, but not speeded initiation, and found expected effects in the kinematic efficiency of this action rather than its initiation time. This finding provides an initial demonstration that goal-relevant, attended self-associated stimuli modulate the unfolding kinematics of action, akin to perceptual match tasks in which stimuli are goal-relevant and attended. Participants’ more direct reach paths toward own-shape cards (versus experimenter’s-shape cards) suggest facilitation of approach actions for self-associated stimuli relative to other-associated stimuli. This seems consistent with

Moradi, Duta, Hewstone, and Humphreys’ (2015) report of increased error rates when a task requires saccades *toward* outgroup-related stimuli or *away* from ingroup-related stimuli. Saccades can be regarded as goal-directed actions. These results suggest there may be a general facilitation of approach-related action and attention for self-associated stimuli. When a task requires goal-directed actions, the interaction of self-association, attention, and motor output may depend heavily on the nature of the goal. Reach-to-grasp paradigms allow flexibility in addressing these issues.

Given that SREs influence unfolding action kinematics, action-related attention effects may provide a way to investigate the degree that SREs interact with attention. For example, distractor stimuli displayed during reaches to targets differentially affect initiation time and trajectory depending on whether they fall within the action space. If self-associated stimuli are processed preattentively, we would expect self-associated distractors to modulate motor parameters across a wider range of space than other-associated or neutral distractors. On the other hand, if SREs require initial top-down allocation of attentional resources, they should be stronger within action space but absent outside of it. Attention paradigms using goal-directed actions in lesion patients will further disambiguate the contribution of vmPFC, pSTS, and fronto-parietal attentional control areas to inhibiting or triggering SREs. Additionally, Humphreys and Sui highlight that the SAN may be particularly important in joint action contexts. Given that joint action often

involves coordinating complex goal-directed actions, understanding how SREs influence goal-directed actions will be important for understanding this link.

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Relevance, valence, and the self-attention network

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Abstract: Consistent with the authors' suggestions for research on extensions beyond the self (e.g., to joint attention and group-related processes), we offer the hypothesis that the Self-Attention Network may facilitate attention to any person who is construed as similar to the self along key dimensions. On the basis of existing literature and our recent findings, we focus on the dimensions of personal relevance and valence. Further research on how these dimensions mediate attention to self and others has the potential to unify separate lines of research on the neural representation of self and others (i.e., social cognition).

On the basis of findings from an array of paradigms, Humphreys and Sui propose a neural network comprised of three nodes that mediates attention to

self-related stimuli. The vmPFC is thought to rapidly respond to self-relevance, feeding forward to the pSTS, resulting in an expectancy bias for future self-related stimuli. This bottom-up network, particularly the vmPFC, is modulated by a frontoparietal control network to allocate attentional resources in accord with task constraints. We believe that this proposal represents a step forward from modular accounts of self-representation in the brain and are optimistic that it will catalyze further research in this area.

Consistent with the authors' suggestions for research on extensions beyond the self (e.g., to joint attention and group-related processes), we offer the hypothesis that the Self-Attention Network may facilitate attention to *any* person who is construed as similar to the self along key dimensions. This hypothesis is grounded in the following observations. Firstly, previous reviews have highlighted the role of cortical midline and frontoparietal regions in representing and evaluating both self and other (Murray, Schaer, & Debbané, 2012; Uddin, Iacoboni, Lange, & Keenan, 2007). Secondly, cortical midline structures have been shown to respond to people and objects bearing some degree of social value (Chen, Welsh, Liberzon, & Taylor, 2010) or personal relevance (D'Argembeau, 2013). Consistent with this picture, behavioral findings from the perceptual matching task developed by Sui and colleagues tend to show a gradient of performance, with well-liked and personally familiar individuals being prioritized over unfamiliar others, albeit to a smaller degree than the self. It is therefore possible that the proposed Self-Attention Network may be recruited in the service of processing any stimulus bearing some degree of social salience, including the self.

Indeed, in a five-identity adaptation of the perceptual matching paradigm (Mattan, Rotshtein, Sumner, & Quinn, *in preparation*), we find that positive non-self identities are prioritized over negative non-self identities (friends and admired celebrities versus enemies and disliked celebrities, respectively) and that personally known non-self identities are prioritized over non-self identities that are not personally known (friends and enemies versus admired celebrities and disliked celebrities, respectively), albeit to a lesser degree than the self. These findings suggest that attentional priority may operate according to gradients of adaptive social dimensions such as valence (e.g., Ma & Han, 2010) and personal relevance (e.g., Adolphs, 2010). Similar dimensions have received much attention in

No potential conflict of interest was reported by the authors.

the social psychology literature (e.g., Fiske, Cuddy, & Glick, 2007; Todorov, Said, Engell, & Oosterhof, 2008); however, these accounts frequently focus on others, to the exclusion of the self. Future work testing the hypothesis that the Self-Attention Network facilitates attention to both self and (similar) others has the potential to unite disparate lines of inquiry, augmenting our understanding of the self and social cognition more broadly.

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Attending to the bodily self

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Abstract: Humphreys and Sui provide a powerful theoretical framework to explain processing biases toward self-related information. However, the framework is primarily applied to information relevant to a *conceptual* self-representation. Here, we show a similar processing bias for information related to the *bodily* self, grounded in sensorimotor representations. Furthermore, we can use bodily illusions to explore the ways in which embodied self-associations can affect our perceptual and attentional processing. It is possible to extend the current framework to take into account these effects, and we argue that this will yield considerable benefits for our understanding of self-relevance.

In the target article, Humphreys and Sui (henceforth H&S) produce a novel framework to explain the effects of self-relevance on attention and perception. H&S base much of their reasoning on findings of processing biases toward arbitrary shapes that have been briefly associated with the self. However, research on the self frequently distinguishes between two forms of self-representation: A “conceptual” self, formed of a rich network of associative and semantic information, and a “bodily” self, grounded in sensorimotor representations (Farmer & Tsakiris, 2012). In this Commentary we discuss the benefits of extending H&S’s framework, which currently focuses primarily on the conceptual self, to encompass the bodily self.

H&S make three key points regarding the effects of self-relevance on attention. First, they present evidence that self-relevant stimuli, e.g., one’s name, show distinct processing advantages in attention and perception. Second, they demonstrate that arbitrary stimuli, such as shapes, can be incorporated into the conceptual self through associative learning. Finally, they show that processing advantages are extended to these newly self-relevant stimuli.

No potential conflict of interest was reported by the authors.

We argue that these points also apply to the bodily self. First, there is considerable evidence of processing bias for information related to the bodily self. For example, sensory integration is enhanced when perceptual stimuli are associated with our own bodies. This enhancement results in increased tactile sensitivity when a visual stimulus is concurrently viewed on our own body (Serino, Pizzoferrato, & Làdavas, 2008) and when auditory stimuli are perceived as close to our body (Làdavas, 2002). Attentional orienting is also altered by bodily self-relevance, with an increased physiological stress response to the sight of painful stimuli approaching one's own body compared to another's body (Guterstam & Ehrsson, 2012).

Secondly, just like the conceptual self, the bodily self is malleable. Synchronous visuotactile stimulation elicits an *embodied* association over non-self-bodies (Botvinick & Cohen, 1998; Tsakiris, 2008). This embodied association also occurs when tactile information is replaced with cardiac information, for example, when viewing a virtual body which is pulsing in synchrony with one's own heartbeat (Aspell et al., 2013).

Finally, once an embodied self-association has been established with another body, the processing advantages previously reserved for one's own body are extended to the other's body. For example, the enhanced integration of visuotactile (Aspell et al., 2013) and audio-tactile (Maister, Cardini, Zamariola, Serino, & Tsakiris, 2015) information is now evident when viewing the other's body. Furthermore, threatening stimuli directed toward the other's body now elicits the same physiological stress responses as threats directed toward one's own body (Farmer et al., 2012).

We argue that neural regions involved in bodily self-representation should be included in H&S's self-attention network. Brain areas such as the anterior insula and temporoparietal junction play a key role both in bodily (e.g., Tsakiris, 2010) and conceptual (Denny, Kober, Wager, & Ochsner, 2012) self-representation, and these areas may support close bidirectional interactions between conceptual and bodily self-relevance (Maister, Slater, Sanchez-Vives, & Tsakiris, 2015). Given the importance of embodied processing in social cognition (Farmer & Tsakiris, 2012; Maister, Slater, et al., 2015), the inclusion of bodily self-processing in the model would extend its explanatory power further into the

social domain, by providing a coherent integrated account of self-relevance.

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