

## From facial cue to dinner for two: the neural substrates of personal choice

David J. Turk,<sup>a,\*</sup> Jane F. Banfield,<sup>b</sup> Bobbi R. Walling,<sup>a</sup> Todd F. Heatherton,<sup>a</sup> Scott T. Grafton,<sup>a</sup> Todd C. Handy,<sup>c</sup> Michael S. Gazzaniga,<sup>a</sup> and C. Neil Macrae<sup>a</sup>

<sup>a</sup>Department of Psychological and Brain Sciences, Center for Cognitive Neuroscience, Dartmouth College, Hanover, NH 03755, USA

<sup>b</sup>Institut für Psychologie II, Otto-von-Guericke-Universität, Magdeburg, Germany

<sup>c</sup>Department of Psychology, University of British Columbia, Vancouver, Canada

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The current experiment examined the neural substrates of response selection, comparing conditions that required participants to make criterion-free selections from sets of same-sex faces (i.e., inconsequential decision) to choosing a dinner date from opposite-sex faces (i.e., consequential decision). In each of these tasks, either a single face (i.e., no choice) or two or three faces (i.e., free choice) appeared for selection. The results revealed that regions of dorsal premotor cortex (PMd) and parietal cortex bilaterally, as well as an area along the medial surface of the superior frontal gyrus, were activated by both consequential and inconsequential decisions, thereby providing evidence for a common selection network. Consequential decisions were further indexed by activation of the insula/ventrolateral prefrontal cortex (BA 47) and the paracingulate gyrus (BA 32). The implications of these findings for current accounts of response selection and social-cognitive functioning are considered.

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*"You have brains in your head. You have feet in your shoes. You can steer yourself any direction you choose. You're on your own. And you know what you know. And YOU are the guy who'll decide where to go." (From: Oh, the places you'll go! Theodor Seuss Geisel, a.k.a. Dr. Seuss, 1990)*

Whether it is selecting a tennis partner, a new car, or items from the breakfast buffet, the ability to make effective choices is central to successful human functioning. Underlying this social-cognitive ability is a range of processing operations, such that selecting one

particular option from an array of competing possibilities involves not only motor processes that carry out the selected action, but also cognitive operations that guide response selection and evaluate the consequences of the chosen item. The goal of the current inquiry is to investigate the neural substrates that support an important aspect of decision making—specifically personal choice. Previous attempts to identify the processes that subserve volitional behavior have provided mixed results (Frith et al., 1991; Grafton et al., 1998) because of subtle differences in the paradigms employed and the possible confounding of choice with working-memory operations (Spence and Frith, 1999). Noting these difficulties, the current research investigated choice-related decision making under conditions in which the influence of working memory was minimized. In addition, extending the theoretical scope of previous work on this topic, the current research considered the consequentiality (i.e., personal relevance) of people's judgments as there is reason to suspect that this factor may be an important moderator of the neural activity that supports decision making (Adolphs, 2001; Frith and Frith, 2003; Gallagher and Frith, 2003; Paulus and Frank, 2003).

### Response selection

Terms such as "free will", "willed action", and "free choice" have been used interchangeably to describe the manner in which people select and execute actions to match the requirements of particular task contexts. Indeed, Jahanshahi and Frith (1998) have defined willed action as "being aware of selecting or rejecting possible responses" (p. 489). Guiding this viewpoint is the notion that volitional behavior (i.e., exercising free will) is more than simply deciding to implement a particular action, it also entails awareness that other responses could have been selected, but were in fact rejected. Frith et al. (1991) and Jahanshahi and Frith (1998), as well as others (Hyder et al., 1997; Spence et al., 1998), have posited that willed action of this kind is supported by a network of brain regions that include dorsolateral prefrontal cortex (DLPFC) and anterior cingulate cortex (ACC). In this model of volitional behavior, response selection is mediated by DLPFC, while ACC is involved in conflict monitoring.

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\* Corresponding author. Department of Psychological and Brain Sciences, Center for Cognitive Neuroscience, Dartmouth College, Moore Hall, Hanover, NH 03755. Fax: +1-603-646-1181.

E-mail address: david.j.turk@dartmouth.edu (D.J. Turk).

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Although implicated in the execution of willed action, the precise functional role played by DLPFC in this process remains open to debate. In their influential article, Frith et al. (1991) instructed participants to move their fingers in an unconstrained manner (i.e., free choice), but with the additional requirement that they do so in a random sequence (i.e., working-memory load). As random generation has been shown to increase activity in DLPFC (Jahanshahi et al., 1997) and is associated with executive processes in working memory (Miyake et al., 2000), this necessarily conflates working-memory operations with response selection, thereby obscuring the functional significance of DLPFC in the generation of volitional behavior. Noting this limitation, recent investigations have attempted to explore willed action in tasks that make equivalent or negligible demands on working-memory resources (Desmond et al., 1998; Spence et al., 1997). In work of this kind, willed action has been accompanied by increased activity in DLPFC, thus suggesting that this structure plays a contributory role in aspects of response selection (see Spence and Frith, 1999).

It is not only the prefrontal and anterior cingulate cortices that are believed to play a prominent role in volitional behavior. Response selection may also be functionally dependent on a cortical network that includes the rostral portion of the dorsal premotor area (PMd—Deiber et al., 1991; Grafton et al., 1998; Passingham, 1985; Sakai et al., 2000; Toni et al., 1999; see also Picard and Strick, 2001 for a review). This region has important connections with the parietal cortex (Petrides and Pandya, 1984) and has been linked to motor preparation (Johnson et al., 1996) and the anticipation of visual cues (Di Pellegrino and Wise, 1991). It is implicated in selection for action and is thought to underpin the execution of higher-level motoric behavior (Spence and Frith, 1999). Given these observations, the current investigation will examine the relative contribution of both premotor and prefrontal cortices to response selection in judgment tasks that vary in their significance (i.e., personal relevance) to people.

### Types of choice

Through investigations of people's random (or otherwise) finger movements in response to stimulation (or the production of words in response to cues), researchers have charted the neural substrates of simple but essentially inconsequential, internally guided behaviors (Frith et al., 1991). Daily life, however, presents people with a range of other decision-making challenges. In particular, response selection is frequently characterized by the need to select an item from an array of competing alternatives (i.e., stimulus-driven choice). Consider, for example, a situation in which one is confronted with the task of selecting a pair of shoes from the multiple options available in a department store. In such a setting, while available choice is enormous, response selection is probably guided (i.e., simplified) by a couple of factors, notably the relevance of the decision to be made (e.g., is being fashionable important to me?) and the potential consequences of one's selection (e.g., will inexpensive hiking boots hurt my feet?). Inspection of the relevant literature reveals that little attention has been directed to the issue of how the consequentiality of the decision to be made may shape the neural correlates of response selection (see Spence and Frith, 1999). Clearly, people can impose their own priorities and preferences on decision making (Goldberg and Podell, 1999; Paulus and Frank, 2003), but what impact, if any, does this have on the neural operations that subserve free choice?

In a recent article, Goldberg and Podell (1999) drew an important distinction between what they termed “veridical” and “adaptive” choices. Veridical responses are akin to selecting the correct option from an array of incorrect alternatives. In contrast, adaptive responses are those in which an individual imposes his or her own set of specific preferences and priorities on an ambiguous situation to guide behavior (e.g., a context in which several responses may be correct). As they then note, “the arsenal of cognitive neuroscience is virtually bereft of paradigms capable of examining how adaptive (as opposed to veridical) decisions are made” (Goldberg and Podell, 1999, p. 366). Deciding which clothes to wear for an interview, whom to invite on a date, or where to take one's summer vacation are judgments in which the responses are decidedly meaningful to people. As such, decision making is likely to be guided by people's preferences and the potential consequences (i.e., costs/benefits) of the competing alternatives. In other words, this type of decision making is criterion based. This then raises an interesting question. Do these additional elements of the decision process increase activation in the same cortical regions that underpin simple, inconsequential decisions (Grafton et al., 1998; Spence and Frith, 1999), or are supplementary regions engaged when people make personally meaningful choices? We explored this important question in the current experiment.

Reflecting the various components of human decision making, one might expect consequential choices to be accompanied by neural activity in cortical regions that support both cognitive and affective aspects of social cognition. Elliott and Dolan (1998), for example, observed activity in medial prefrontal cortex (MPFC) when participants were requested to select one of two abstract stimuli. In task settings of this kind, preference judgments may recruit areas of MPFC that track with self-referential mental activity (Kelley et al., 2002; Macrae et al., in press), notably, establishing one's preferred option from a range of competing alternatives (see Frith and Frith, 2003; Gallagher and Frith, 2003; Paulus and Frank, 2003). As Adolphs (2001) has noted, areas of prefrontal cortex play a pivotal role in executive (i.e., higher order) aspects of social cognition, such as response selection and the volitional control of behavior. As such, one might expect activity in these regions to subserve people's consequential decisions when competing options are available.

In addition, activity may also be expected in areas of the brain that are associated with the evaluative aspects of response selection. According to recent theorizing (Bechara et al., 1997; Damasio et al., 1996), stimuli induce an internal state that is associated with pleasurable or aversive somatic markers. In turn, these markers serve to guide people's behavior towards pleasurable outcomes. Neuroimaging investigations have suggested that the insula plays an important functional role in preference judgments with obvious hedonic implications (Paulus and Frank, 2003); hence, one might expect activity in this structure to be modulated by the consequentiality of people's choices (Adolphs, 2001; Bechara, 2002; Damasio, 1994, 1996). Finally, as volitional action entails not only response selection, but also competitor suppression (Jahanshahi and Frith, 1998), it is possible that cortical regions associated with cognitive inhibition may also be implicated in the execution of free choice, especially in consequential task contexts. Paradigms that specifically measure response inhibition, such as the Go/No-Go task, have identified regions of ventrolateral prefrontal cortex (VLPFC) that track with response suppression (Anderson et al., 2004). Furthermore, patients with damage to this region are

generally impulsive and have difficulty inhibiting inappropriate responses (e.g., Horn et al., 2003; Verfaellie and Heilman, 1987). Given these observations, it is possible that areas of VLPFC may also subserve people's consequential choices when competing alternatives are available.

To summarize, the current experiment has two objectives: (i) to determine the neural substrates of choice and (ii) to identify brain regions that track with the consequentiality of people's judgments. To explore these issues, neural activity was measured while participants viewed varying numbers of faces and selected either a dinner date (i.e., consequential choice) or an arbitrary same-sex target (i.e., inconsequential choice).

## Methods

### Participants

Eighteen right-handed, heterosexual participants between the ages of 18 and 35 (nine men and nine women; mean age, 22 years) were recruited from the local Dartmouth community. Participants reported no significant abnormal neurological history and all had normal or corrected-to-normal visual acuity. Participants were either paid for their participation or received course credit. All participants gave informed consent in accordance with the guidelines set by the Committee for the Protection of Human Subjects at Dartmouth College.

### Image acquisition

Imaging was performed on a 1.5-T whole body scanner (General Electric Medical Systems Signa, Milwaukee, WI) with a standard head coil. Visual stimuli were generated using an Apple G3 laptop computer running PsyScope software (Cohen et

al., 1993). Stimuli were back projected to participants with an Epson (model ELP-7000) LCD projector on a screen positioned at the head end of the bore. A fiber optic, light-sensitive keyboard with four keys interfaced with the PsyScope Button Box (New Micros, Dallas, TX) was used to record participants' behavioral responses. Cushions were used to minimize head movement.

Anatomical images were acquired using a high-resolution 3D spoiled gradient recovery sequence (SPGR; 128 sagittal slices; TE = 3 ms, TR = 7 ms, flip angle = 15°, voxel size = 1 × 1 × 1.2 mm). Functional images were collected in runs using a gradient spin-echo, echo-coplanar sequence sensitive to BOLD contrast (T2\*) (TR = 2500 ms, T2\* evolution time = 35 ms, flip angle = 90°, 3.75 × 3.75 mm in-planer resolution). During each functional run, 64 sets of axial images (25 slices; 4.5-mm slice thickness, 1-mm skip between slices) were acquired allowing complete brain coverage.

### Behavioral tasks

An event-related fMRI protocol was used to collect BOLD data. Participants were scanned during six functional runs that consisted of three functional runs of inconsequential-choice trials (selecting a same-sex face), and three functional runs of consequential-choice trials (selecting a dinner date from an array of opposite-sex faces). The run order was counterbalanced across participants using an ABBAAB design. Each run consisted of 64 events; comprising 12 zero-choice trials, 12 two-choice trials, 12 three-choice trials, and 28 fixation trials presented in a fixed-random order. Fixation trials invariably consisted of four black square plates presented across the horizontal axis in the center of the screen. These plates were directly mapped onto the response keys so that the plate to the far left mapped on to the leftmost key. At the zero-choice level, a single face appeared and the corresponding key had to be pressed.

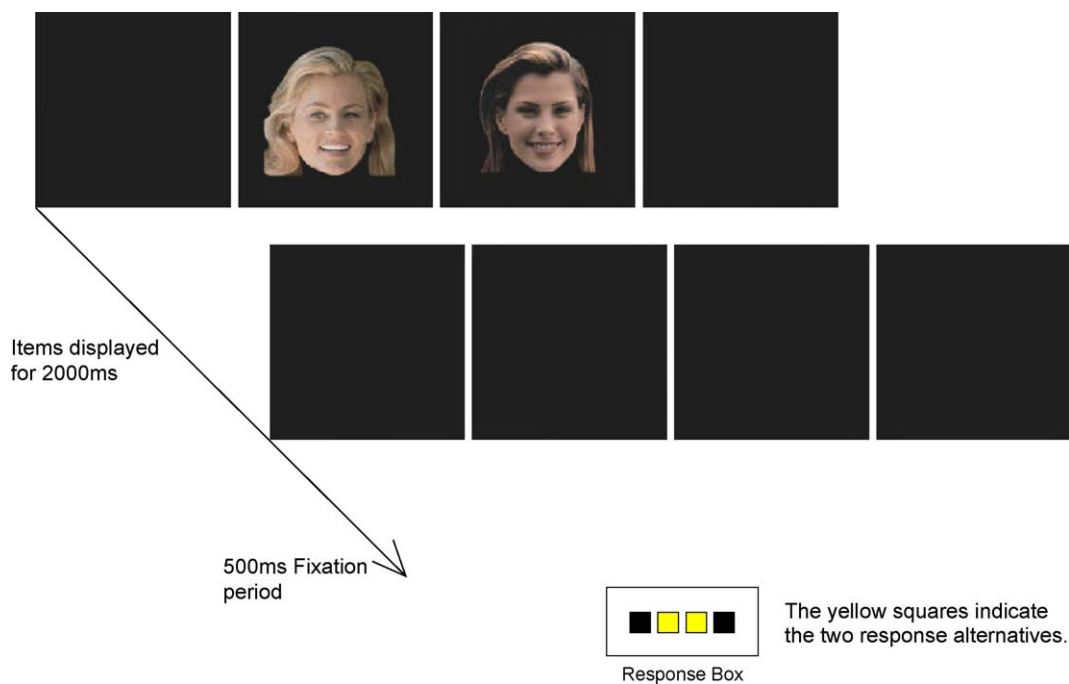


Fig. 1. Schematic representation of one event.

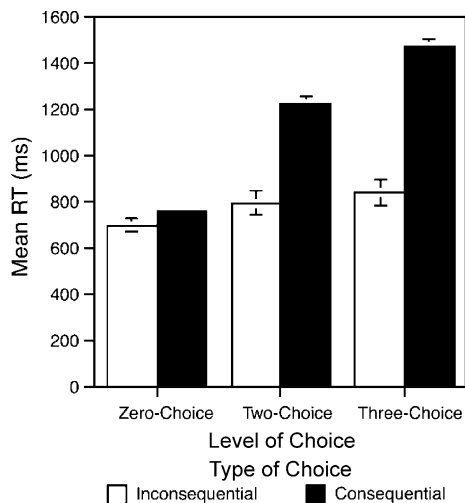


Fig. 2. Response latencies (ms) for the type of choice by level of choice interaction.

In the two-choice condition, two faces appeared and participants had to select one of two competing responses. In the three-choice condition, selection of one of three competing faces was required. In the consequential-choice condition, participants were told to select one item from the array and to make their selection on the basis of their preferred choice of dinner date. In the inconsequential-choice condition, participants were told to select any face from the array. We examined personal choice by comparing criteria-free responses to faces (same-sex faces) with the selection of a dinner date (opposite-sex faces). Each trial consisted of four black plates in which one, two, or three faces appeared. The stimuli were presented for 2000 ms before returning to the fixation-state (see Fig. 1). All responses were made with the right hand.

#### Data analysis

The fMRI data were analyzed using Statistical Parametric Mapping (SPM99, Wellcome Department of Cognitive Neurology,

London, UK; Friston et al., 1995). For each functional run, data were screened for sources of noise or artifact. Functional data were corrected for differences in acquisition time between slices for each whole-brain volume, realigned within and across runs to correct for head movement, and coregistered with each participant's anatomical data. Functional data were then transformed into a standard anatomical space (2 mm isotropic voxels) based on the ICBM 152 brain template (Montreal Neurological Institute), which approximates Talairach and Tournoux's (1988) atlas space. Normalized data were then spatially smoothed (8 mm full width half maximum [FWHM]) using a Gaussian kernel. Analyses took place at two levels: formation of statistical images and regional analyses of hemodynamic responses.

First, for each participant, a general linear model, incorporating task effects (modeled with a canonical set of three functions: the hemodynamic response function; the temporal derivative; and its dispersion derivative; Friston et al., 1998), mean, linear, cubic, and quadratic trends were used to compute parameter estimates ( $\beta$ ) and  $t$  contrast images (containing weighted parameter estimates) for each comparison at each voxel. These individual estimates were then submitted to a second-level, random-effects analysis to create mean  $t$  images (threshold at  $P = 0.001$ , uncorrected; minimal cluster size = 10). An automated peak search algorithm identified the location of peak activations and deactivations based on the  $z$  value and cluster size. This analysis allowed both within- and between-condition comparisons to be made (e.g., [CHOICE > NO-CHOICE] or [DATE > FACE]).

A masking analysis was employed to determine common brain networks that support both consequential and inconsequential choice. These regions may therefore provide evidence for a response selection network irrespective of the type of choice to be made. This was done using the ImCalc feature in SPM, and according to the following formula: [(condition 1  $t$  score > 3.65)  $\times$  (condition 2  $t$  score > 3.64)]. This procedure yields a mask containing only those voxels that were significantly activated above  $t = 3.65$  ( $P < 0.001$ ) in each and both contrasts. The resulting mask provided information about the extent of the overlapping activations associated with the conditions involved. This mask was then applied to the contrast

Table 1  
Inconsequential and consequential choice

Region	Talairach coordinates left hemisphere					Talairach coordinates right hemisphere				
	K value	x	y	z	Z max	K value	x	y	z	Z max
<i>Inconsequential choice</i>										
Medial surface of superior frontal gyrus (BA 8)						15	4	18	51	3.79
Dorsal premotor cortex (BA 6)	21	-20	7	62	3.73	50	20	3	52	4.11
Ventral premotor cortex (BA 6)	50	-48	6	33	4.57	10	48	-7	22	3.70
Occipitotemporal cortex	546	-39	-71	-13	5.46	596	20	-78	-13	6.09
Parietal cortex						21	38	-56	54	4.74
<i>Consequential choice</i>										
Medial surface of superior frontal gyrus (BA 8)	602	0	18	47	extending to right PMd					
Dorsal premotor cortex (BA 6)	99	-32	-9	63	4.30	24	-1	63	4.50	
Ventral premotor cortex (BA 6)	22	-44	2	33	3.76	45	48	5	26	4.72
Occipital/parietal/temporal cluster	1721	-44	-63	-10	5.68	40	-78	-3	5.42	
Insula/VLPFC	139	-36	27	-5	4.64	108	32	27	-5	5.61

Summary of the significant results for response selection in both the FACE and DATE tasks. Threshold,  $P < 0.001$ .

Table 2  
Common brain regions activated by inconsequential and consequential choice tasks

Region	Talairach coordinates left hemisphere					Talairach coordinates right hemisphere				
	K value	x	y	z	Z max	K value	x	y	z	Z max
Medial surface of superior frontal gyrus (BA 8)						10	4	18	51	4.34
Dorsal premotor cortex (BA 6)	13	–24	–1	55	3.79	32	20	3	51	4.31
Occipitotemporal cortex	436	–39	–71	–13	5.57	532	20	–78	–13	5.76
Parietal cortex						14	28	–56	54	4.43

Summary table of common regions activated by the FACE and the DATE tasks. Mean Z scores for the DATE > FACE and FACE > DATE contrast are presented in the table.

Threshold,  $P < 0.001$ .

image files for each participant and a group analysis was then performed on the masked data (DATE > FACE or FACE > DATE) to provide a table of the common clusters across both choice conditions.

## Results

### Behavioral data

Response latencies for each type and level of choice were analyzed using a 2 (type of choice: consequential or inconsequential)  $\times$  3 (level of choice: zero or two or three) repeated measures analysis of variance (ANOVA). This revealed main effects of type of choice [ $F(1,17) = 116.345$ ,  $P < 0.0001$ ], level of choice [ $F(2,34) = 157.3$ ,  $P < 0.0001$ ], and a type of choice  $\times$  level of choice interaction [ $F(2, 34) = 126.43$ ,  $P < 0.0001$ ]. The interaction showed that (i) participants responded more rapidly on inconsequential than consequential trials and (ii) for both types of choice, increasing the number of possible responses increased response latency, but this effect was most pronounced for consequential judgments (see Fig. 2).

### fMRI data

Analysis of the imaging data focused on two specific questions. First, is there a common network of brain regions engaged in the

execution of both consequential and inconsequential choice? Second, is consequential choice indexed by the recruitment of additional cortical regions or by an increased BOLD response in same areas that subserve choice per se? To address these issues, three specific contrasts were performed: (i) choice (three faces and two faces) > no choice (one face) in the FACE condition; (ii) choice (three faces and two faces) > no choice (one face) in the DATE condition; and (iii) DATE (consequential choice) > FACE (inconsequential choice). In the group analyses, all contrasts were thresholded at a  $t$  value of  $P < 0.001$  (uncorrected), with a minimum cluster size of 10 contiguous voxels.

### The neural correlates of response selection

The significant clusters for the activation maps for the first two contrasts (i.e., regions that show a higher BOLD response for the three-choice and two-choice conditions compared with the zero-choice condition for both consequential and inconsequential choice) are shown in Table 1.

A masking analysis revealed common regions of activation across both consequential and inconsequential choice (see Table 2). These included portions of the occipital cortex extending dorsally to the posterior parietal cortex bilaterally, a region around the intersection of the precentral sulcus and the superior frontal sulcus, which we have labeled the dorsal premotor region (PM<sub>d</sub>—BA 6), and the medial surface of the superior frontal gyrus (BA 8—pre-SMA).

Table 3  
Contrasting inconsequential and consequential choice

Region	Talairach coordinates left hemisphere					Talairach coordinates right hemisphere				
	K value	x	y	z	Z max	K value	x	y	z	Z max
<i>DATES &gt; FACES</i>										
Insula/VLPFC (BA 47)	26	–32	23	–1	3.85	57	36	23	–1	4.51
Medial surface of the superior frontal gyrus (BA 8)	47	8	6	51	3.76					
Dorsal ACC (BA 8/32)							8	25	3	3.53
Paracingulate gyrus (BA 32)						10	0	40	16	3.49
Fusiform gyrus (BA 37)						16	40	–59	11	3.86
Occipital cortex/fusiform gyrus (BA 18)						11	36	–74	0	3.56
<i>FACES &gt; DATES</i>										
Occipital cortex extending into posterior fusiform gyrus (BA 18)	119	–40	–67	–13	4.92	114	24	–74	–6	4.82

Regions showing significant BOLD increases for the contrast.

DATE (3 and 2 > zero) > FACE (3 and 2 > zero).

Threshold,  $P < 0.001$ .



The neural correlates of consequential decisions

Our second question pertained to the degree to which consequential choice may be indexed by the recruitment of additional cortical regions, or by a higher BOLD response in the same regions that subserves choice. To examine this issue, we contrasted the BOLD responses for the consequential and inconsequential decisions (see Table 3). Consequential choice was indexed by a higher BOLD response in seven clusters. These contrast-specific regions are made up of areas that show BOLD activation for both consequential and inconsequential choices (as described above), and those that only show increased activity for consequential decisions. Regions that appear to respond to both consequential and inconsequential decisions

include the occipitotemporal cortex, fusiform gyrus, and the medial surface of the superior frontal gyrus. In addition, the dorsal portion of the anterior cingulate cortex (BA 8/32) also seems to be active for both consequential and inconsequential decisions. These areas show greater BOLD responses for the DATE condition, but the FACE condition also shows a significant hemodynamic response function (see Fig. 3).

The remaining foci of activation in the DATE > FACE contrast included bilateral regions of the anterior insula/ventrolateral prefrontal cortex (BA 47) and the paracingulate gyrus (BA 32). The BOLD response for inconsequential decisions was at a subthreshold level in these regions as demonstrated by the FACE contrast. The timecourse data show that in these regions, the BOLD response was not modulated by the amount of

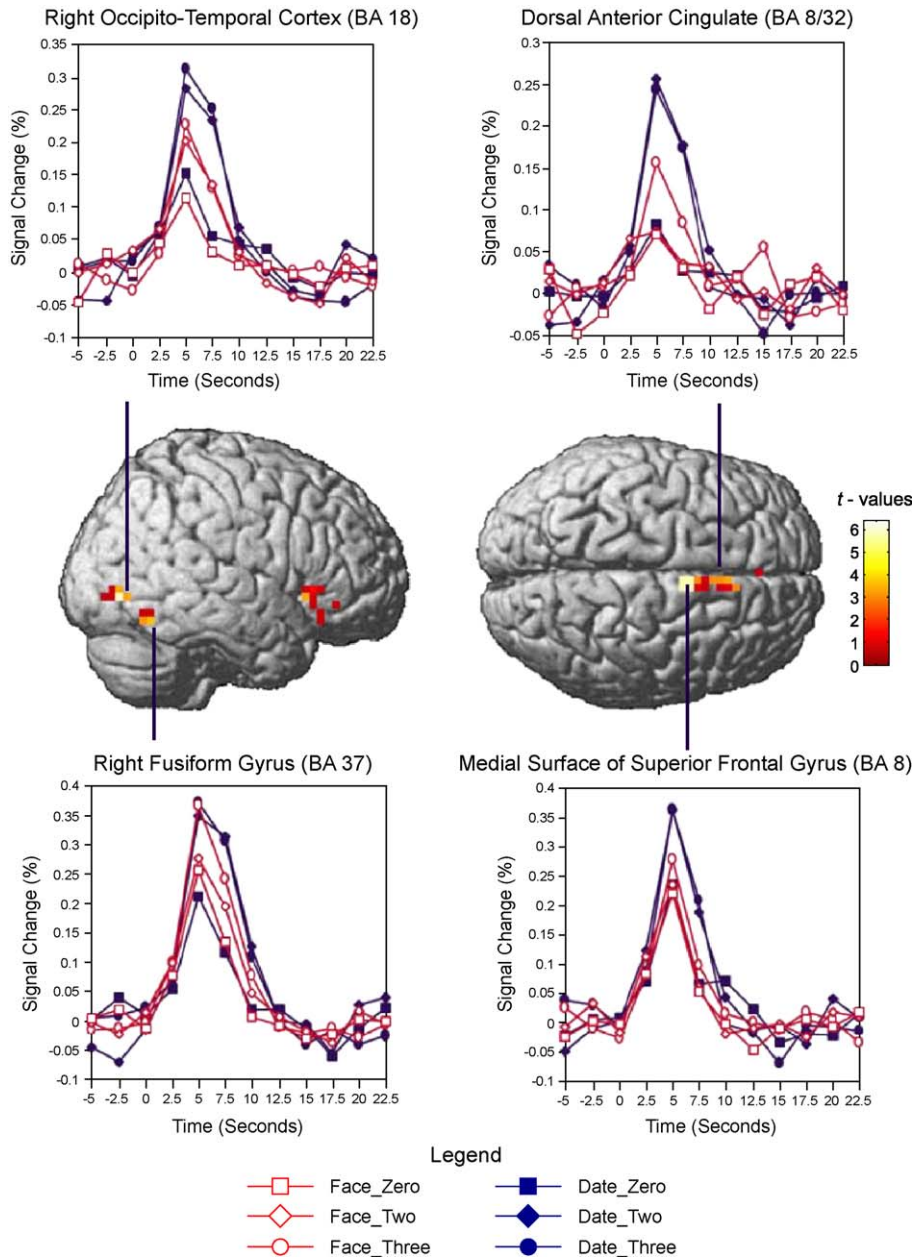


Fig. 3. Contrast for DATE > FACE. Regions that show significantly higher BOLD response for DATE, but which still show BOLD responses to FACE above baseline.

available choice. That is, these regions show significant activation for any level of choice in the consequential condition (see Fig. 4). The FACE > DATE contrast revealed significantly greater hemodynamic response in two bilateral regions of the occipitotemporal cortex including the posterior fusiform gyrus.

*Gender effects in consequential choice*

To explore if the sex of participants moderated the neural activity associated with date selection (Goldberg and Podell, 1999), we further analyzed the consequential choice data using a two-sample *t* test. This contrast showed no significant regions of activation for the female > male contrast, but did reveal a region that was significantly more active for male than female

participants. This region was part of the superior parietal cortex (BA 7) (20, -76, 41). Importantly, however, no significant differences were observed in the frontal regions identified in Table 3.

**General discussion**

The current research had two basic objectives: (i) to identify the neural substrates of choice and (ii) to determine if additional regions of the brain are involved in consequential (i.e., personally relevant) decisions. With regard to the first of these issues, the results revealed common regions of the dorsal premotor cortex (PMd), the medial surface of the superior frontal gyrus (BA 8), and

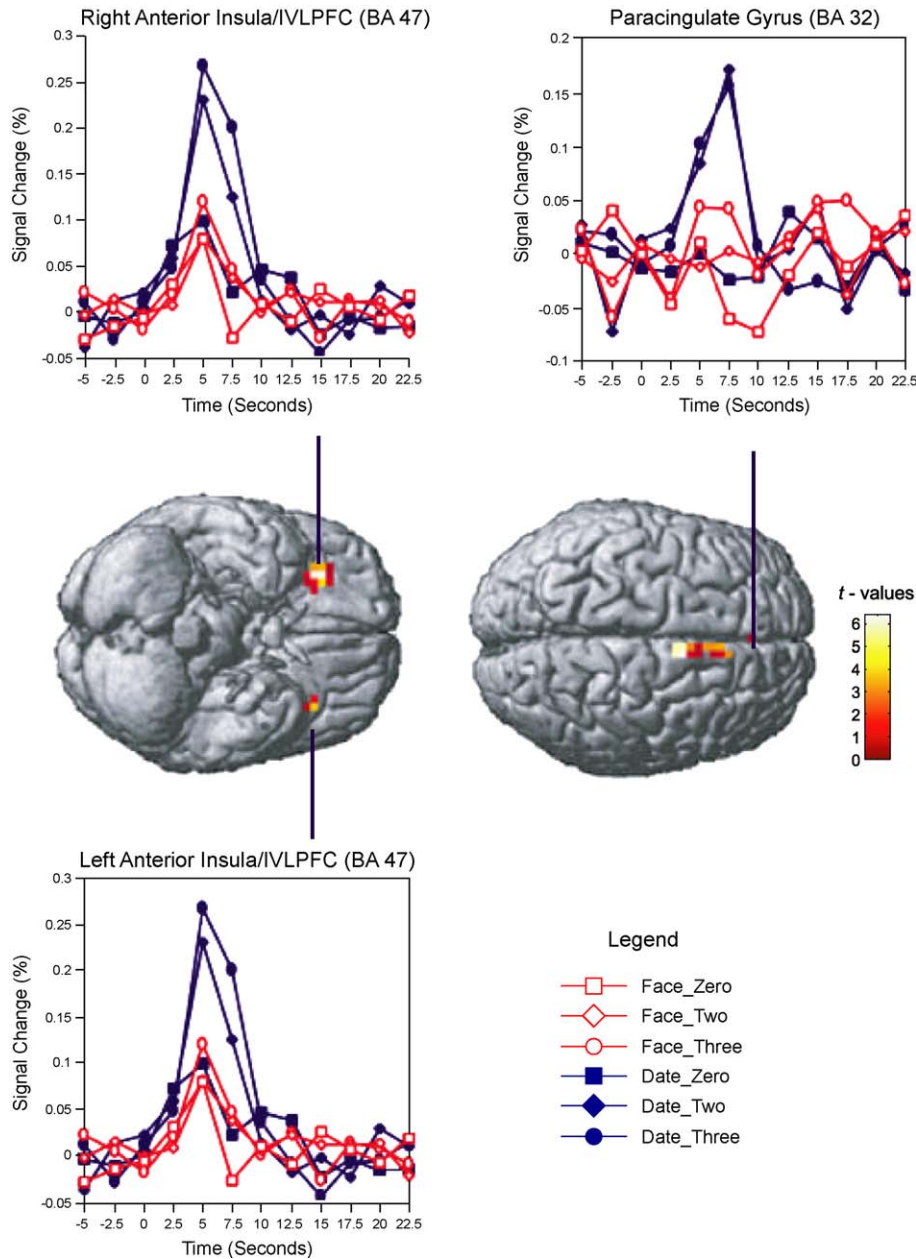


Fig. 4. Contrast for DATE > FACE. Regions that show significantly higher BOLD response for DATE, but show no significant BOLD increases in the FACE condition.

the posterior parietal cortex that showed higher levels of activation in the choice than no-choice conditions, regardless of the judgment under consideration (Jenkins et al., 1992; Mushiaki et al., 1991). The observed activity in this parietal-PMd network is consistent with other work of this kind and identifies these areas as the cortical loci of response selection (Deiber et al., 1991; Grafton et al., 1998; Passingham, 1985; Sakai et al., 2000; Spence et al., 1997). Importantly, however, response selection was not accompanied by increased activity in DLPFC. This implies that prior research demonstrating the recruitment of this area in free choice may have been a consequence of the working-memory demands (e.g., random generation) of the tasks under investigation (Frith et al., 1991; Hyder et al., 1997). It is possible therefore that DLPFC may only be implicated in volitional behavior when the demands of the task necessitate that multiple items (e.g., current options, competing alternatives, previous responses) be retained or manipulated in temporary storage (Desmond et al., 1998; Fuster, 1995; Hadland et al., 2001).

Extending previous work on this topic, the current inquiry also considered the extent to which response selection may be moderated by the nature of the decision under consideration (i.e., inconsequential vs. consequential). The results of this comparison revealed two distinct patterns of activation: regions that showed higher activity for consequential decisions, but were also above threshold for inconsequential decisions, and regions in which activity was specific to consequential judgments. Brain regions that showed greater BOLD response for consequential than inconsequential decisions included two areas of the right ventral temporal cortex, dorsal ACC, and the medial surface of the superior frontal gyrus or pre-SMA (BA 8). These ventral temporal regions located around the putative fusiform face area (Kanwisher et al., 1997) are presumably associated with increased face processing in the consequential-choice condition (i.e., selecting a dinner date).

Activity in the ACC has been associated with task monitoring and the detection of conflict (Ernst et al., 2001; MacDonald et al., 2000). When one is faced with the task of choosing an item from several alternatives, conflict inevitably ensues. The magnitude of this conflict, however, would appear to be related to the judgment at hand. The hemodynamic response in ACC was elevated when the judgment was consequential (i.e., criterion-based) rather than arbitrary (i.e., criterion-free). Interestingly, the dorsal anterior cingulate has strong connections with the SMA, premotor cortex, and parietal cortex (Bush et al., 2000), areas that were also found to be active in the current experiment (see Table 2). Activation of ACC during response selection is also consistent with previous studies on willed action (Frith et al., 1991). The current findings therefore offer support for a network of regions including the parietal cortex, premotor cortex, and ACC in response selection and evaluation (Adolphs, 2001).

Of additional theoretical importance, several brain areas were only active during consequential decisions. These included bilateral portions of the insula/ventrolateral prefrontal cortex (BA 47) and the paracingulate gyrus (BA 32). Activation of the insula has been observed in a range of studies investigating aspects of emotional processing. One suggested role for the insula is that it indexes autonomic changes that take place in the body during the processing of emotive stimuli (Damasio, 1994, 1996). In this way, insula activation can be taken as a marker of people's preference for specific stimuli (e.g., attractive faces—Nakamura et al., 1998). Paulus and Frank (2003), for example, reported activity in this region when participants were required to select a preferred item

from two competing alternatives (e.g., types of soft drink). Thus, in addition to aversive events (Chua et al., 1999) and negative emotional material (Morris et al., 1998; Phillips et al., 1998), the anterior insula also appears to be involved in processing contexts that may have positive consequences for perceivers, such as selecting a beverage or a dinner date (Adolphs, 2001; Bechara, 2002; Damasio, 1994, 1996; Paulus and Frank, 2003). In addition, the ventral frontal activity observed in the DATE > FACE contrast may also index response inhibition (Anderson et al., 2004). If, during criterion-based decision making (e.g., selecting a dinner date), more than one target is a plausible candidate, decision making may be supported by inhibitory processes that suppress possible but nonselected options.

Importantly, consequential choice was also accompanied by increased activity in the paracingulate gyrus. Recent research has identified this structure as a critical component of the cortical network that supports Theory of Mind (i.e., mentalizing—see Frith and Frith, 2003; Gallagher and Frith, 2003). As Gallagher and Frith (2003) have observed, “several functional imaging studies have been undertaken to isolate the neural substrates of mentalizing ability. These have demonstrated remarkably consistent results . . . this ability is mediated by a highly circumscribed region of the brain, the anterior paracingulate cortex” (p. 78). Interestingly, areas of MPFC have also been shown to play a critical functional role in self-referential mental activity, such as reporting one's personality characteristics (Kelley et al., 2002; Macrae et al., *in press*). The activation of the paracingulate gyrus during consequential decision making (i.e., selecting a dinner date) provides further support for the importance of prefrontal regions in fundamental aspects of social-cognitive functioning. Selecting a potential dinner date likely entails a combination of mentalizing (e.g., “I wonder what she's like?”) and self-referential processing (e.g., “have I been successful with blondes in the past?”), operations that are supported by activity in regions of MPFC (Frith and Frith, 2003).

In considering the observed patterns of neural activity for consequential and inconsequential decisions, a potential limitation with the current paradigm must be acknowledged. Whereas inconsequential judgments were always undertaken on same-sex faces, opposite-sex faces were used to trigger participants' consequential decisions. It might be argued therefore that the resultant neural activity is indicative of stimulus-driven effects (i.e., judging opposite-sex faces), rather than the personal relevance of the judgments that were furnished. Although the available neuroimaging literature on this topic is quite limited, discrete effects appear to emerge when people process attractive, opposite-sex faces (see Senior, 2003). In particular, facial attractiveness is associated with activity in regions of the brain that are associated with the reward value of stimuli, such as the orbitofrontal cortex (O'Doherty et al., 2003), the nucleus accumbens (Aharon et al., 2001), and the insula (Nakamura et al., 1998). As can be seen from the timecourse data in Fig. 4, the current results do not simply reflect the neural activity that accompanies the processing of attractive opposite-sex faces. For the observed bilateral activity in the insula, the BOLD response in the inconsequential condition (viewing same-sex faces) was similar to that found in the consequential condition (viewing opposite-sex faces) at the zero-choice level. That is, viewing both same and opposite-sex faces modulated activity in this region. Importantly, however, only when participants were required to choose between two or more opposite-sex faces (i.e., consequential choice) was there a significant increase in the BOLD signal. This would suggest that consequential choice is an important moderator



of neural activity in the insula during preference-related decision making.

In sum, at least as indexed in the current investigation, response selection appears to be reliant on a network of cortical regions that include the parietal cortex, dorsal premotor cortex, pre-SMA, and dorsal areas of the ACC (Deiber et al., 1991; Grafton et al., 1998; Passingham, 1985; Sakai et al., 2000; Schluter et al., 2001; Toni et al., 1999; see also Picard and Strick, 2001 for a review). Supplementing these regions are additional frontal areas, including the anterior insula/VLPFC and the paracingulate gyrus, that are implicated in the execution of consequential judgments. Daily life confronts people with a variety of decisions, some trivial, others consequential. When competing possibilities are available, response selection appears to be supported by activity in regions of the dorsal premotor cortex (PMd) and the posterior parietal cortex, cortical areas that are insensitive to the nature of the judgment at hand. When a decision is personally meaningful or emotionally salient, however, additional frontal areas are recruited. Activity in these areas (e.g., insula, paracingulate gyrus) likely tags the hedonic relevance and personal significance of stimuli for people, thereby facilitating response selection in the future.

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